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The vascular anatomy and comparative morphology of apocynaceous flowers

ROBERT E. WOODSON, JR., AND JOHN ADAM MOORE
(WITH PLATES 3–5 AND 72 FIGURES)

Although systematic research in the anatomy of flowers dates from the classic investigations of Philippe Van Tieghem (1875) in the last quarter of the past century, the subject cannot be said to have attained prominence in the field of plant anatomy until approximately the past ten years. Within that period the lively discussions of floral anatomy which have been waged, particularly in England and the United States (Eames, 1931; Saunders, 1925) with respect to the merits or demerits of the polymorphic interpretation of crucifer carpels and those of other families of angiosperms has stimulated research concerning the general vascular structure of the flower in many of the important botanical laboratories of the world. Since the flower has been the principal basis of classification of all modern systems of the flowering plants, it is not unnatural that those botanists whose great desire it is to approach ever closer an approximation of evolution have turned to the research of floral anatomy as a timely and promising means to that end.

When the senior author of these observations commenced the taxonomic study of Apocynaceae somewhat over ten years ago, the first papers concerning floral anatomy had just begun to issue from the laboratories of Professor Eames of Cornell University, shortly to be followed by those of Miss Saunders of Cambridge, England. Such approaches to the study of the flower appeared so attractive and significant that an investigation of the floral anatomy of Apocynaceae was immediately begun. From this beginning an account of the vascular anatomy of the genera *Apocynum* and *Nerium* was published in 1930. It was not until several years later that the writer chanced upon a previous and more general account of the floral anatomy of *Apocynum* by Grelot (1897), with which his views were in general agreement.

In the years that have intervened, flowering material of 39 genera and 60 species of Apocynaceae, representing all subdivisions of the family in its distribution in both hemispheres, has been obtained from living specimens in botanic gardens and in the field through the efforts of the senior author and numerous friends to whom he is greatly indebted. Herbarium specimens, although available for such studies within the natural limitations due to desiccation, were employed only in a few critical genera extremely difficult to obtain in the field, such as the polycarpellary genus

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Pleiocarpa of tropical Africa. In general, serial transverse and longitudinal sections approximately 10μ thick were prepared according to the familiar alcohol-xylol-paraffin schedule, and stained in crystal violet and erythrosin, or fast green and safranin.

During the academic year 1935–36 the senior author of these observations was aided by the technical services of his former student, Dr. John Adam Moore, through a grant of the Science Research Fund of Washington University (St. Louis) provided by the Rockefeller Foundation.

REPRESENTATION OF GENERA AND SPECIES

Names preceded by an asterisk (*) denote material obtained from herbarium specimens; all others obtained fresh, and fixed in formalin-acetic-alcohol.

Subfamily PLUMERIOIDEAE

Acocanthera spectabilis Hook.
Allamanda cathartica L.
Amsonia ciliata Walt.
Carissa Carandas L.
C. grandiflora A. DC.
Cerbera Tanghin Hook.
**Cufodontia Stegomeris* Woods.
Haplophyton cimicidum A. DC.
Lacmellia edulis Karst.
Lochnera rosea (L.) Reichb.
**Pleiocarpa bicarpellata* Stapf
**P. mutica* Hook.
Plumeria rubra L.
Plumeriopsis Ahouai (L.) Rusby & Woods.
Rauwolfia tetraphylla L.
Rhazya orientalis (Dcne.) A. DC.
Stemmadenia Alfari (Donn. Sm.) Woods.
S. grandiflora (Jacq.) Miers
S. obovata (Hook. & Arn.) K. Sch.
Tabernæmontana acutissima Muell.-Arg.
T. arborea Rose
T. chrysocarpa Blake
T. Cumingiana A. DC.
T. divaricata R. Br.
Thevetia peruviana (Pers.) K. Sch.
Vinca major L.
V. minor L.
Zschokkea panamensis Woods.
Z. ramosissima Muel.-Arg.

Subfamily ECHITOIDEAE

Adenium coetenium Stapf
Beaumontia grandiflora Wall.
Cycladenia humilis Benth.
Forsteronia viridescens Blake
Funtumia elastica (Preuss) Stapf
Macrosiphonia Brachysiphon (Torr.) Gray
M. Macrosiphon (Torr.) Heller
Malouetia guatemalensis (Muell.-Arg.) Standl.
Mandevilla Bridgesii (Muell.-Arg.) Woods.
M. hirsuta (A. Rich.) K. Sch.
M. illustris (Vell.) Woods.
M. laxa (R. & P.) Woods.
Mascarenhasia elastica K. Sch.
Mesechites trifida (Jacq.) Muell.-Arg.
Nerium Oleander L.
Odontadenia Hoffmannseggiana (Steud.) Woods.
O. Schippii Woods.
Prestonia acutifolia (Benth.) K. Sch.
P. portobellensis (Beurl.) Woods.
Rhabdadenia biflora (Jacq.) Muell.-Arg.
Strophanthus dichotomus A. DC.
S. gratus A. DC.
S. sarmentosus A. DC.
**Thenardia Galeottiana* Baill.
Trachelospermum difforme (Walt.) Gray
T. jasminoides (Lindl.) Lem.
Urechites Andrieuxii Muell.-Arg.

Subfamily APOCYNOIDEAE

Apocynum androsaemifolium L.
A. cannabinum L.
Trachomitum venetum (L.) Woods.

GENERAL MORPHOLOGY OF THE FLOWER

The apocynaceous flower is always tetracyclic, and is pentamerous save in three small tetramerous genera. The calyx is barely gamosepalous in the majority of instances, the lobes being cleft nearly to the receptacle. The aestivation is almost invariably imbricated. The chief interest in the calyx of Apocynaceae lies in the frequent presence of small, glandular processes, known as "squamellae," which are found within, at the base of the lobes (cf. figs. 2, 5, 8).

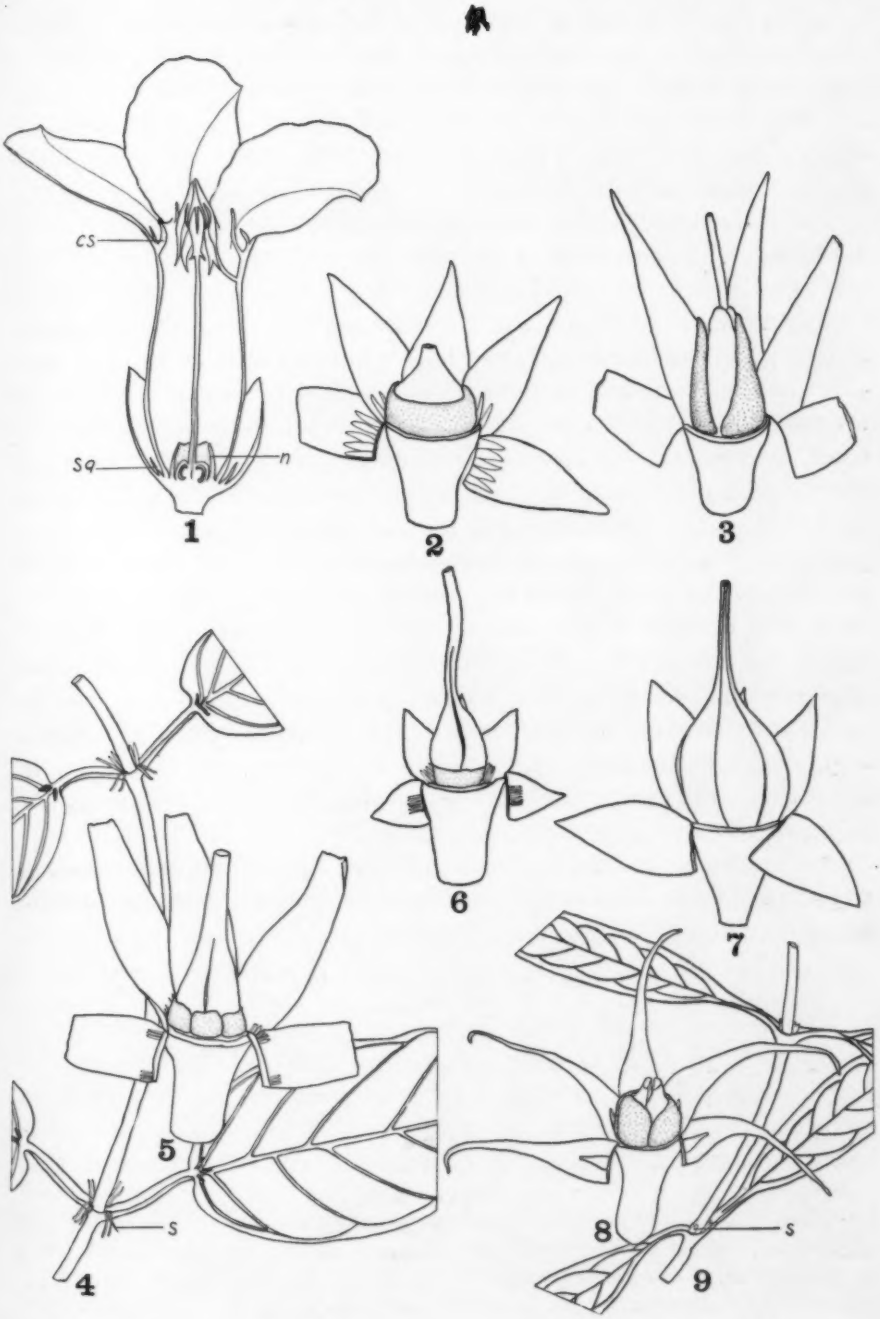
The corolla is gamopetalous and actinomorphic throughout the family, and displays a wide assortment of campanulate, salverform, infundibuli-

form, and rotate modifications. The aestivation is contorted. As in the calyx, the chief interest in the corolla is found in the occasional genera which bear various internal appendages, known as "corolline scales," which form structures strongly reminiscent of the corolline coronas of many Asclepiadaceae (cf. figs. 22, 23, 24). In certain genera, as *Strophanthus* and *Nerium*, the corolline scales may be conspicuously exserted and petaloid, while in others, as *Apocynum*, they may constitute exceedingly inconspicuous, basal emergences which may be observed only after dissection.

The stamens of Apocynaceae are always epipetalous and alternate with the corolline members. Although exceedingly diversified in their morphology and histology, the stamens offer little of interest from the standpoint of vascular anatomy. Nevertheless, the construction and relationship of the anthers has been found extremely practical in the separation of subfamilies: The Plumerioideae are distinguished by anthers without sterile, basal appendages and are not connivent nor agglutinated to the stigma; both the Echitoideae and the Apocynoideae have basally appendiculate anthers which are usually connivent and agglutinated to the stigma through the secretion of certain peculiar, glandular cells. The unique relation of the anthers and stigmata of Echitoideae and Apocynoideae has prompted the suggestion that those families may be more "advanced" than the Plumerioideae, perhaps representing a transition to Asclepiadaceae (Demeter, 1922). Such considerations, however, are without the scope of these studies which are concerned chiefly with vascular anatomy and interpretive gross morphology.

The ovary of Apocynaceae may be either apocarpous or syncarpous. When apocarpous, the ovary is usually bicarpellary, each carpel being infolded at the margins to form an axile, binate placenta. The two free carpels converge at the tips to form a common stylar shaft surmounted by a common, usually rather massive stigma (cf. fig. 1; pl. 5, fig. 6). Among the Apocynaceae with apocarpous ovaries are found a group of three or four genera, designated as the tribe Pleiocarpeae, which are characterized by as many as five free carpels. In such polycarpellary gynoecia each carpel contributes directly to the style and stigma (cf. fig. 7).

Figs. 1–9. Fig. 1., longitudinal section, flower of *Prestonia portobellensis: sq*—squamella, *n*—nectary, cs—corolla scales; fig. 2, calyx and gynoecium of *Thevetia peruviana;* fig. 3, calyx and gynoecium of *Lochnera rosea;* fig. 4, vegetative branch of *Mandevilla Bridgesii: s*—stipular appendages; fig. 5, calyx and gynoecium of *Mandevilla Bridgesii*; fig. 6, calyx and gynoecium of *Tabernaemontana chrysocarpa;* fig. 7, calyx and gynoecium of *Pleiocarpa mutica;* fig. 8, calyx and gynoecium of *Thenardia Galeottiana;* fig. 9, vegetative branch of *Thenardia Galeottiana: s*—stipular appendages.


cs
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Among the syncarpous Apocynaceae both bilocular and unilocular bicarpellary ovaries are encountered. In the bilocular, the placentation of each cavity is axile and binate; in the unilocular ovaries are found two opposed, linear, parietal placentae (cf. pl. 5, figs. 1, 2). In either event the ovary is characterized by a common stylar shaft surmounted by the stigma in the usual manner for the family.

From the standpoint of these investigations, the chief interest in the gynoecium of Apocynaceae is found in the cycle of "nectaries" or "disc lobes" which surrounds the ovaries of many genera. These structures are usually more or less fleshy, and adopt a variety of modifications: chiefly as clusters of discrete bodies, two to five in number (cf. figs. 3, 5), or as collar-like or sleeve-like rings of tissue (cf. figs. 2, 6), about the base of the ovary. Although smaller than the carpels which they surround in most cases, the nectaries occasionally simulate the carpels not only in general shape, but in size as well. Although they frequently are more or less adnate to the ovary, they are always free from the style.

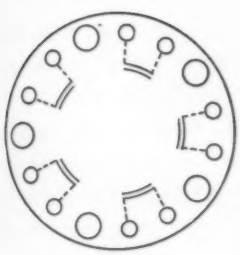
Although appearing to be quite superior in ordinary dissections, the ovaries of many Apocynaceae are more or less "subinferior," or immersed for a short distance within the receptacle. In the genera *Plumeria* (pl. 5, fig. 5) and *Himatanthus* this immersion is found to a marked degree, almost rendering the gynoecium completely inferior.

In order to avoid needless repetition, observations on the floral anatomy of the genera and species will be considered, not separately, but under headings of the various component structural units, such as pedicel, calyx, corolla and androecium, and gynoecium. This method not only is convenient but is justifiable since the flower, considered anatomically, is a condensed short shoot system bearing at the nodes appendages of differing structural and functional modifications.

ANATOMY OF THE PEDICEL

The pedicel of all known Apocynaceae contains an amphiphloic siphonostele (pl. 3, fig. 1) agreeing in general with that of the young stem. The internal phloem of certain genera demonstrates in the pedicel and receptacular stele a marked tendency to separate into small strands which leave the inner face of the protoxylem, from which they are frequently

Figs. 10–21. Calyx anatomy of various Apocynaceae: calyx midribs indicated by large circles, calyx laterals by smaller circles, corolla midribs by squares, residual stele by double arcs, derivation of traces by broken single lines, centripetal succession of calyx lobes by numerals: fig. 10, *Lacmellia edulis;* figs. 11–12, *Mandevillas ubsagittata;* figs. 13–14, *Mandevilla hirsuta;* fig. 15, *Tabernaemontana chrysocarpa;* fig. 16, *Thevetia peruviana;* figs. 17–21, *Rauwolfia tetraphylla.*



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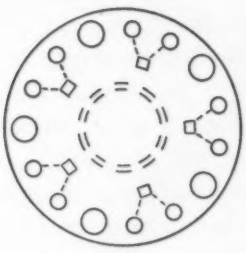

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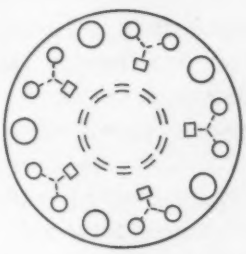

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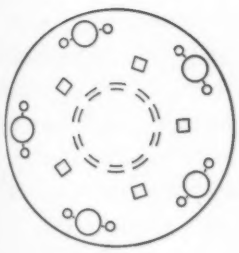

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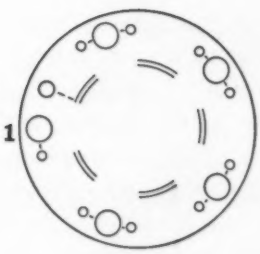

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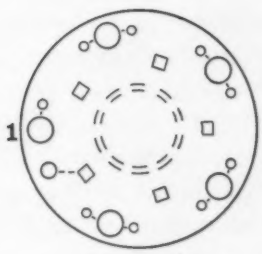

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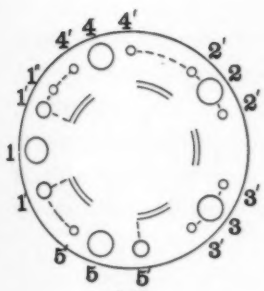

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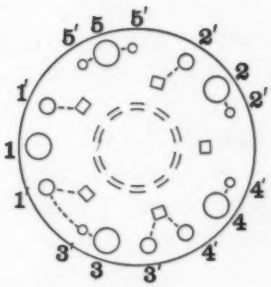

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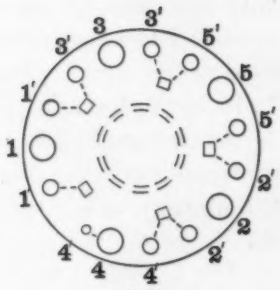

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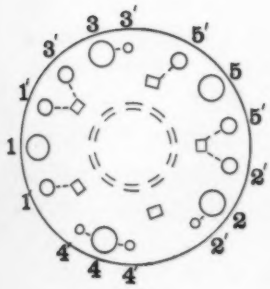

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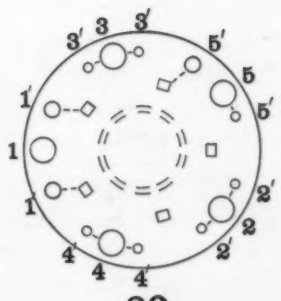

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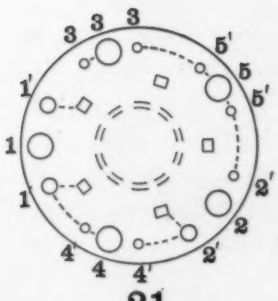

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isolated by a few cells of basic parenchyma, and invade the pith, where they branch and anastomose irregularly (pl. 3, figs. 1, 2) as described by Scott and Brebner (1891) for the stems or roots of certain Gentianaceae, Apocynaceae, Asclepiadaceae, Solanaceae and Plumbaginaceae. In the apocynaceous flowers which we have investigated, it may be observed usually that the invasion of the pith by strands of internal phloem is perhaps most accentuated immediately before the departure of the calycine traces, after which the former are eliminated either by recombination with the normal internal phloem or by passage and combination outward with the traces to the calyx.

The internal phloem of apocynaceous flowers apparently consists chiefly of protophloem parenchyma, with but few poorly developed sieve tubes. The parenchyma is so similar in appearance to poorly developed provascular tissue that it scarcely comes as a surprise to find that in some cases it may behave similarly to the latter in differentiating into isolated, spiral tracheids (pl. 3, fig. 2). This phenomenon has been found in the pedicels not only of such Apocynaceae as *Tabernaemontana acutissima*, *Stemmadenia grandiflora*, and *Odontadenia Schippii*, but occasionally in certain gentianaceous flowers as well. The provascular tendency of the internal phloem of the pedicellar stele is quite probably to be correlated with the appearance of "meristems producing secondary, medullary wood" discovered by Scott and Brebner (1891) in the stems of *Apocynum cannabinum* L., *Willughbeia firma* Bl. (Apocynaceae), and *Periploca graeca* L. (Asclepiadaceae).

Similar to the internal phloem, the external phloem evidently consists principally of parenchyma in the pedicel. The outer is more uniform than the inner, however, and maintains its position immediately external to the xylem.

The pedicellar wood consists chiefly of protoxylem with a relatively scant development of metaxylem and secondary xylem. Vessels apparently are never present, and the secondary walls of the tracheids are either spiral or annular. Fibers never occur such as have been found in the flowers of certain Gentianaceae (Woodson, 1936).

The organization of latex tissues within the pedicel, as within the flower as a whole, is extremely diversified, to such an extent that observations concerning the laticiferous, storage, and secretory systems will be ignored in this account, possibly to be treated more fully in a subsequent paper.

VASCULAR ANATOMY OF THE CALYX

In the lower receptacle of all apocynaceous flowers the pedicellar stele, usually roughly circular in outline at first, becomes more or less sharply

5- or 10-lobed. In the former case, the lobes are identical with the decurrent midribs of the five calyx lobes. Alternating with these five lobes, the five additional in the 10-lobed stele indicate in most instances the positions of the corolline midribs (cf. fig. 53). As one would expect, the first series of traces to depart from the pedicellar stele are those destined to supply the calyx. For general purposes the calyces of all known Apocynaceae may be divided into four types of organization with respect to their nodal anatomy:

Type I. In the calyces included under Type I the midribs depart from the receptacular stele leaving in each case a single gap. Then, before the stele has again united, the margins of the five gaps give off a single trace, ten in all, which are the lateral traces of the calyx lobes (fig. 10). These lateral traces are therefore coherent to the margins of the gaps left in the stele by the departure of the calyx midribs, and the nodal anatomy in each case is essentially a 3-trace, 1-gap system. Both midrib and laterals soon give rise to small subsidiary veinlets of decreasing magnitude as they progress toward the tips of the calyx lobes.

Various modifications of the typically symmetrical nodal anatomy obtain, frequently in different flowers from the same inflorescence. For example, the lateral traces of each calyx lobe may depart from the receptacular stele to which they are coherent somewhat before the departure of the midribs. Occasionally one margin of the gap left by a midrib may produce no lateral trace, giving rise to a 2-trace condition which may proceed to the tip of the calyx lobe.

The condition of this type may be recognized as basically 3-trace, 1-gap, with the laterals coherent separately to the margins of the midrib gaps *before the organization of the corolline traces*. It appears probable, in view of the widespread opinion that the 3-trace condition is primitive for both vegetative and floral appendages (Sinnott, 1914; Eames, 1931), that the apocynaceous calyces included within Type I are the most "primitive" from the structural standpoint. It is interesting to note in this connection that the vegetative nodes of all known Apocynaceae produce a single trace from which the laterals are subsequently derived.

Genera and species showing various modifications of the Type I calyx vascular skeleton include:

Lacmellia edulis Karst.
Malouetia guatemalensis (Muell.-Arg.) Standl.
Stemmadenia Alfari (Rose) Woods.
S. grandiflora (Jacq.) Miers
S. obovata (Hook. & Arn.) K. Sch.
Tabernaemontana acutissima Muell.-Arg.
T. arborea Rose.

Features of vascular organization in varying extents similar to Type I, but which are asymmetrically combined with other types, will be discussed under Type IV. It may be of phylogenetic significance that all the genera enumerated above are referable to the subfamily Plumerioideae, save *Malouetia*, which is ordinarily included within the Echitoideae although it was placed in an intermediate position by Mueller (1860).

Type II. The second type of calyx, with respect to vascular anatomy, includes those species in which the lateral traces of the lobes are adnate to the base of the corolline midribs. In this type, the departure of the calyx midribs is immediately followed by the organization of the five midribs to the corolla lobes. Soon after the differentiation of the corolline midribs from the receptacular stele, the adnation of the calyx laterals is terminated, and either the two laterals of adjacent calyx lobes depart separately from the single, alternate corolla midrib (fig. 11), or the two cohere mutually for a short distance after their common severence from the corolline trace (fig. 12). When the calyx laterals are adnate separately to the corolline midrib or cohere mutually for a short distance appears relatively insignificant, as the two conditions may be found usually in the same species, if more than one specimen be examined.

Type II is significant, however, in so far as the 3-trace condition found in Type I evidently is more elaborate, progressing from cohesion to the receptacular stele proper to adnation to the corolla midrib. Genera and species illustrating various modifications of the Type II calyx skeleton include:

Amsonia ciliata Walt.
Carissa Carandas L.
C. grandiflora A. DC.
Forsteronia viridescens Blake
Funtumia elastica (Preuss) Stapf
Haplophytum cimicidum A. DC.
Lochnera rosea (L.) Reichb.
Mandevilla subsagittata (R. & P.) Woods.
Rhabdadenia biflora (Jacq.) Muell.-Arg.
Rhazya orientalis (Dcne.) A. DC.
Tabernaemontana Cumingiana A. DC.
T. divaricata R.Br.
Thenardia Galeottiana Baill.
Trachelospermum difforme (Walt.) Gray
T. jasminoides (Lindl.) Lem.
Urechites Andrieuxii Muell.-Arg.
Vinca major L.
V. minor L.

If this enumeration is compared with the classification of the Apocynaceae studied during this investigation (p. 136), it will be seen that the genera included above are referable to both subfamilies Plumeroideae and Echitoideae in equal proportions.

Type III. The simplest type of vascular anatomy found in apocynaceous calyces is found in Type III, in which each calyx lobe is strictly 1-trace. This midrib departs from the receptacular stele quite regularly, later giving rise to laterals upon either side, in a manner which is predominant amongst the majority of Gamopetalae (fig. 13). This simple calyx skeleton is found throughout the various taxonomic divisions of the Apocynaceae, and is quite possibly more "advanced" phylogenetically than either Type I or Type II. Genera and species illustrating this type include:

Adenium coetenium Stapf
Allamanda cathartica L.
Apocynum androsaemifolium L.
A. cannabinum L.
Cerbera Tanghin Hook.
Cycladenia humilis Benth.
Mandevilla hirsuta (A. Rich.) K. Sch.
M. illustris (Vell.) Woods.
M. splendens (Hook.) Woods.
Meschites trifida (Jacq.) Muell.-Arg.
Nerium Oleander L.
Pleiocarpa bicarpellata Stapf
P. mutica Benth.
Plumeria rubra L.
Plumeriopsis Ahouai (L.) Rusby & Woods.
Prestonia acutifolia Benth.
P. portobellensis (Beurl.) Woods.
Strophanthus dichotomus A. DC.
S. gratus A. DC.
S. sarmentosus A. DC.
Tabernaemontana chrysocarpa Blake
Trachomitum venetum (L.) Woods.

Even this type is not entirely free from variation, however, since occasionally a single lateral is found to proceed from either the margin of the gap left in the receptacular stele by the departing calyx midrib (fig. 14) as in Type I, or from the corolline midrib (fig. 15) as in Type II.

Type IV. For the purpose of exposition, Type IV is most easily considered after the three preceding types. Actually, however, it is intermediate between all three, incorporating features of Types I and III, or

of Types II and III. In this type of calyx skeleton the vascular supply to the five lobes is distinctly asymmetrical, certain of the lobes receiving their traces according to Type I or Type II, and the others according to Type III. Something of phylogenetic value may be adduced from the fact that the outer lobes are more prone to Types I or II than are the inner, which are somewhat more likely to show Type III (figs. 16–21 inclusive).

The impetus to this condition may be the strong imbrication of the calyx lobes of many genera and species, the inner frequently being more or less completely enclosed within the outer, the two series becoming somewhat different in appearance. This tendency is well marked in the genus *Odontadenia*, and culminates in the remarkable calyx of *Cufodontia*, unparalleled amongst known Apocynaceae (in which the two or three outer lobes become connate, completely hiding the smaller pair within).

Genera and species showing various modifications of the Type IV calyx skeleton include:

(*Combination of Types I and III*)

Beaumontia grandiflora Wall.
Macrosiphonia Brachysiphon (Torr.) Gray
Mascarenhasia elastica K. Sch.
Odontadenia Hoffmannseggiana (Steud.) Woods.
O. Schippii Woods.
Thevetia peruviana (Pers.) K. Sch.
Zchokkea panamensis Woods.
Z. ramosissima Muell.-Arg.

(*Combination of Types II and III*)

Mandevilla Bridgesii (Muell.-Arg.) Woods.
M. laxa (R. & P.) Woods.
Rauwolfia tetraphylla L.

The vagaries of this type may be illustrated best by a few individual species, considering a single flower for each. For, as will be shown in the case of *Rauwolfia tetraphylla*, one may obtain almost any conceivable mixture of the types by examining a number of flowers from a single inflorescence.

Thevetia peruviana (fig. 16). Outermost calyx lobe (1)[1] similar to Type I, with the laterals cohering to the margins of the midrib gap, *but each lateral branching within the receptacle to form the adjacent laterals of the neighboring lobes* (4–5). Of the remaining lobes, two (2–3) are essentially like Type III, giving rise to their own laterals, but in the case of one of

[1] The parenthetical numerals refer to the succession of lobes as visualized in the ideographs, progressing centripetally, from 1 to 5.

these (2), one forks to give rise to the lateral of the lobe to the left (4), similarly to the type of cohesion seen in the outermost lobe (1). In the case of the innermost lobe (5) one lateral is produced from the adjacent lateral of the outermost lobe, while the other coheres to the margin of the midrib gap according to the situation found in Type I. In this flower of *Thevetia*, therefore, an odd mixture of Types I and III exists in addition to three puzzling instances of cohesion of adjacent laterals of neighboring lobes.

Rauwolfia tetraphylla (figs. 17–21 inclusive). The variation shown in calyces of the Type IV vascular system is well shown in *Rauwolfia tetraphylla*. From a single inflorescence of this species preserved in alcohol for the senior writer by the late Dr. N. L. Britton upon his last trip to Puerto Rico, twelve flowers were selected for comparison. Each of these twelve calyces demonstrated a different combination of Types II and III, together with cohesions similar to those found in *Thevetia peruviana*.

Five variations of the calyx skeleton of this species are diagrammed in figures 17–21 inclusive. In figure 17 a peculiar cohesion is illustrated involving the right (as seen from within) lateral of lobe 1, with the left lateral and the midrib itself of the adjacent lobe 3. A precisely similar cohesion is found in figure 21 involving lobes 1 and 4; furthermore this skeleton is complicated by cohesions involving the adjacent right and left laterals of lobes 2 and 4 respectively, while the laterals of lobe 5 are both coherent to the laterals of adjacent lobes 3 and 2.

The striking variability of the calyx anatomy of Type IV genera and species is somewhat of a deterrent to the direct correlation of vegetative and floral nodal anatomy. At the same time, an impetus should be given to the study of variation in floral anatomy, a field that has appeared to at least some observers to be in imminent danger of "too easy" interpretations. On the other hand, the derivation of the 1-trace from the basic 3-trace condition is decidedly clarified by the very existence of transitions.

THE NATURE OF THE CALYCINE SQUAMELLAE

The most interesting feature of the apocynaceous calyx from the standpoint of comparative morphology is the occurrence of the internal glands, or "squamellae." The position, numbers, and aspect of these small structures are sufficiently constant and characteristic to be of importance taxonomically. There are three chief categories of squamellae with respect to their relationships with the calyx lobes which they subtend: *alternate* with the lobes, upon the margins of which they appear to be attached, either singly or in groups (fig. 5), *opposite* the lobes, solitary (fig. 8) or

in groups (fig. 6), or *indefinitely distributed*, when they seem to form a fringe of many individuals uniformly distributed around the very base of the calyx (fig. 2). Although squamellae are frequent in the family, they are occasionally lacking (figs. 3, 7).

It is significant to note that the vegetative nodes of most Apocynaceae also bear small, frequently glandular structures at the base of the petioles. As in the squamellae, these nodal appendages may be either alternate, opposite, or indefinitely distributed with respect to the petiole. Although the Apocynaceae are usually considered as an exstipulate family, these appendages are doubtless in the category of stipules, following the interpretation of Glück (1919). As one studies the Apocynaceae, one cannot fail to observe the fact that the position of the squamellae with respect to the calyx lobe is in most cases quite similar to that of the appendages of the vegetative node with respect to the petiole (cf. figs. 4, 5; 8, 9). One would be justified in assuming from this evidence the two categories to be equivalent, and the calycine squamellae as stipules.

This observation upon gross morphology is substantiated materially by studies of microscopic anatomy. As seen in longitudinal (pl. 3, fig. 7) or transverse section (pl. 4, fig. 6), the squamellae are found to consist of a small core of somewhat elongated cells continuous with the mesophyll of the calyx lobe which they subtend, surrounded by a glandular epidermis of horizontally compressed cells usually containing a nucleus in the region nearest the "core." Vascular tissue usually is lacking, but in such species as *Strophanthus gratus* (pl. 4, fig. 6) and *Funtumia elastica* (pl. 4, fig. 5) small bicollateral bundles derived from the marginal venation of the calyx lobe are found to be present, simulating the vascular supply of many stipules (Sinnott and Bailey, 1914). Both from the standpoint of gross morphology and from the vascular anatomy of certain species, therefore, the stipular nature of the squamellae appears well substantiated.

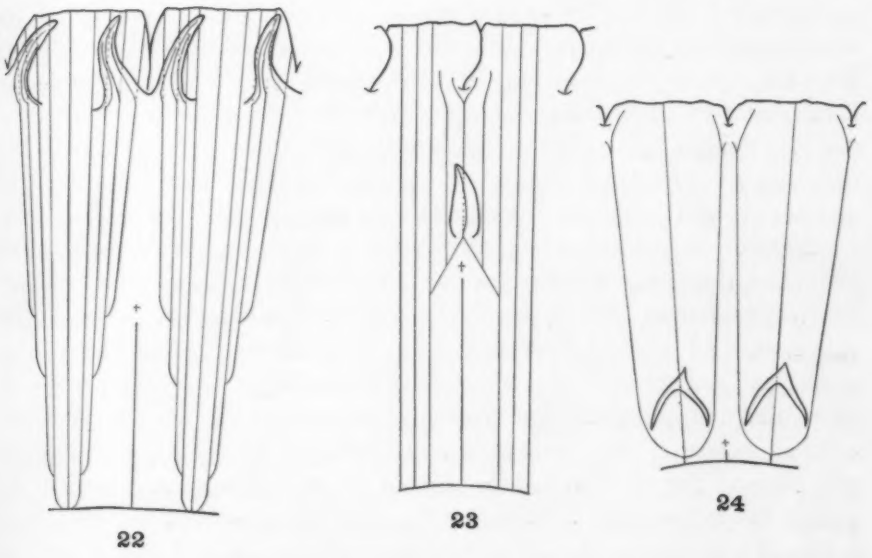
As in the case of normal, marginal stipules, the alternate type of squamellae would appear basic. The solitary, opposite squamella would appear to have been derived by the fusion of two marginal squamellae in a position adaxial to the calyx lobe which they subtend. Evidence to support this assumption is found in serial sections of such a flower as that of *Mandevilla subsagittata* (pl. 4, figs. 3–4), in which the very base of the opposite squamella is found to be bipartite and related to the margins of the calyx lobe. The indefinitely distributed squamellae are explainable with justification merely by assuming the developmental laceration of either alternate or opposite members.

The foliar nature of the calycine squamellae of Apocynaceae therefore appears fairly obvious, according to Glück's (1919) observations from

gross morphology, and in contradiction to Woodson's (1930) previous interpretation of these organs as possibly staminodia, a position, adopted entirely upon the basis of adenopetaly in double flowers of *Nerium Oleander*, which must now be discarded.

VASCULAR ANATOMY OF COROLLA AND ANDROECIUM

The nodal anatomy of the corolla of Apocynaceae is relatively simple. To each of the normally five lobes of the gamopetalous corolla a single trace departs from the receptacular stele after the differentiation of the calycine midribs. Almost at the same time five alternate traces are produced for the five epipetalous stamens. An exception to this general con-



Figs. 22–24. Morphology and vascular anatomy of the corolla scales of certain Apocynaceae: fig. 22, *Strophanthus sarmentosus;* figs. 23, *Prestonia portobellensis;* fig. 24, *Apocynum androsaemifolium*. The point of attachment of stamens is indicated as +

dition is found in the investigated species of *Apocynum* and *Trachomitum* (figs. 53–57 inclusive), both members of the subfamily Apocynoideae, in which the staminal traces are briefly adnate to the midribs of the opposite calyx lobes.

The chief feature of interest as far as the general vascular anatomy of the corolla is concerned is the adnation of the calyx laterals to the corolline midribs in certain genera and species, which already has been discussed. Lateral venation is obtained in the corolla merely by the more or less

frequent branching of the midrib. The staminal bundles remain unbranched throughout their adnation to the corolla as well as throughout the staminal filaments and the anthers.

The curious anatomy of the anthers is a topic of interest because of the extreme variation of cellular modification. Since this subject deals exclusively with modifications of the fundamental tissues, however, it will be deferred for the present, perhaps to be treated in a future paper on the reproductive mechanism of the family.

THE NATURE OF THE COROLLINE SCALES

The chief morphological interest in the corolla of Apocynaceae lies in the faucal appendages or "corolline scales" occasionally found within the gamopetalous tube. These appendages frequently are showy and laminate, forming a fringe or "corona" within the throat of the corolla from which they may be widely exserted. In such genera as *Strophanthus* (fig. 22) these scales occur in pairs alternate with the corolla lobes. In *Prestonia* (fig. 23) a single appendage occurs immediately above the insertion of the stamens. In *Apocynum* (fig. 24) they are inconspicuous and scale-like, and adnate to the base of the corolla tube and opposite the lobes.

The corolline scales of apocynaceous corollas apparently are never glandular, the organization of the fundamental tissues being in all essential respects similar to that of the corolla proper. Furthermore certain of the scales, such as those of *Apocynum* and *Trachomitum*, contain no vascular tissue, and one might be led to consider them simply as emergences of no particular morphological significance. In the majority of such appendaged corollas, however, the presence of well developed vascular tissues may be proved, and the skeletal relationship of the appendages and the corolla proper easily observed by clearing the whole corolla in lactic acid. Diagrams of segments of three representative corollas treated in this manner are provided in figures 22–24 inclusive.

Strophanthus sarmentosus (fig. 22) possesses paired faucal appendages alternate with the corolla lobes. In cleared corollas the vascular bundles traversing each appendage are found to be derived from the outermost lateral veins of the adjacent corolla lobe. Furthermore it is found that the traces entering the appendage are merely branches of the corolline laterals which proceed up into the corolla lobe. When compared with the gross morphology and vascular anatomy of such a stipulate node as that of *Pelargonium* (Sinnott and Bailey, 1914) it appears obvious that the corolline scales of *Strophanthus* must be interpreted as stipules.

An interesting modification of the corolline appendage is found in species of *Prestonia* (fig. 23), which is solitary and alternate with the

corolla lobes. In the case of *P. portobellensis* a single vascular strand is found within the scale. But this strand has been formed by the fusion of branches from the outermost lateral vein of both adjacent corolla lobes, the veins themselves continuing up into the respective corolla lobes. This condition is decidedly similar to that of the single interpetiolar stipules of many Rubiaceae. Far from being an "exstipulate family," therefore, the Apocynaceae are seen to bear stipules not only at the vegetative nodes, but subtending the members of both calyx and corolla as well. Both the calyx and the corolla of this family are evidently foliar.

VASCULAR ANATOMY AND COMPARATIVE MORPHOLOGY OF THE GYNOECIUM

The gynoecium of Apocynaceae is more diversified than is generally understood. Normally it is bicarpellary, the ovary proper being apocarpous or syncarpous. When apocarpous, each carpel possesses an infolded, marginal placenta bearing few to numerous ovules. When syncarpous, the component carpels may adhere more or less closely by their commisural margins, but maintaining their individuality to create a bilocular ovary, each loculus containing an axile, binate placenta similar to that found in apocarpous ovaries (pl. 5, fig. 1).

When unilocular, however, the ovary contains two parietal placentae oriented horizontally to the position of the two axile placentae of the bicarpellary ovary (pl. 5, fig. 2). In frequent instances one finds that a syncarpous ovary is bilocular at both base and apex, where placentation is axile, but unilocular in the middle where placentation is parietal. The natural inference from such a simple observation is that the unilocular condition has been derived from the bilocular phylogenetically as well as ontogenetically, by the cohesion of contiguous placental margins of the component carpels, and the separation of the component halves of the erstwhile binate placentae. The simple process by which this coexistent cohesion and separation may be accomplished is obvious when one observes in bilocular, syncarpous ovaries that the closely appressed epidermal layers of the infolded margins composing the axile placentae of either carpel retain their distinction long after the epidermis separating the two carpels themselves has been obliterated.

Another proof of the two parietal placentae as consisting of fused halves of adjacent axile placentae is found in the orientation of the vascular bundles contained within the common stylar shaft uniting the carpels. The styles of bicarpellary Apocynaceae invariably contain two separate bundles which are the prolongations of the respective carpellary midribs. In the styles of bilocular ovaries the orientation of the bundles

is in the same diameter with respect to the axile placentae (cf. figs. 51–52; 71–72), but invariably at a deviation of roughly 90° with respect to the parietal placentae (cf. figs. 69–70). This simple observation should at once explain the derivation of parietal from axile placentae and confound the attempt to explain the "commisural stigma" upon the basis of "carpel polymorphism (Saunders, 1925)."

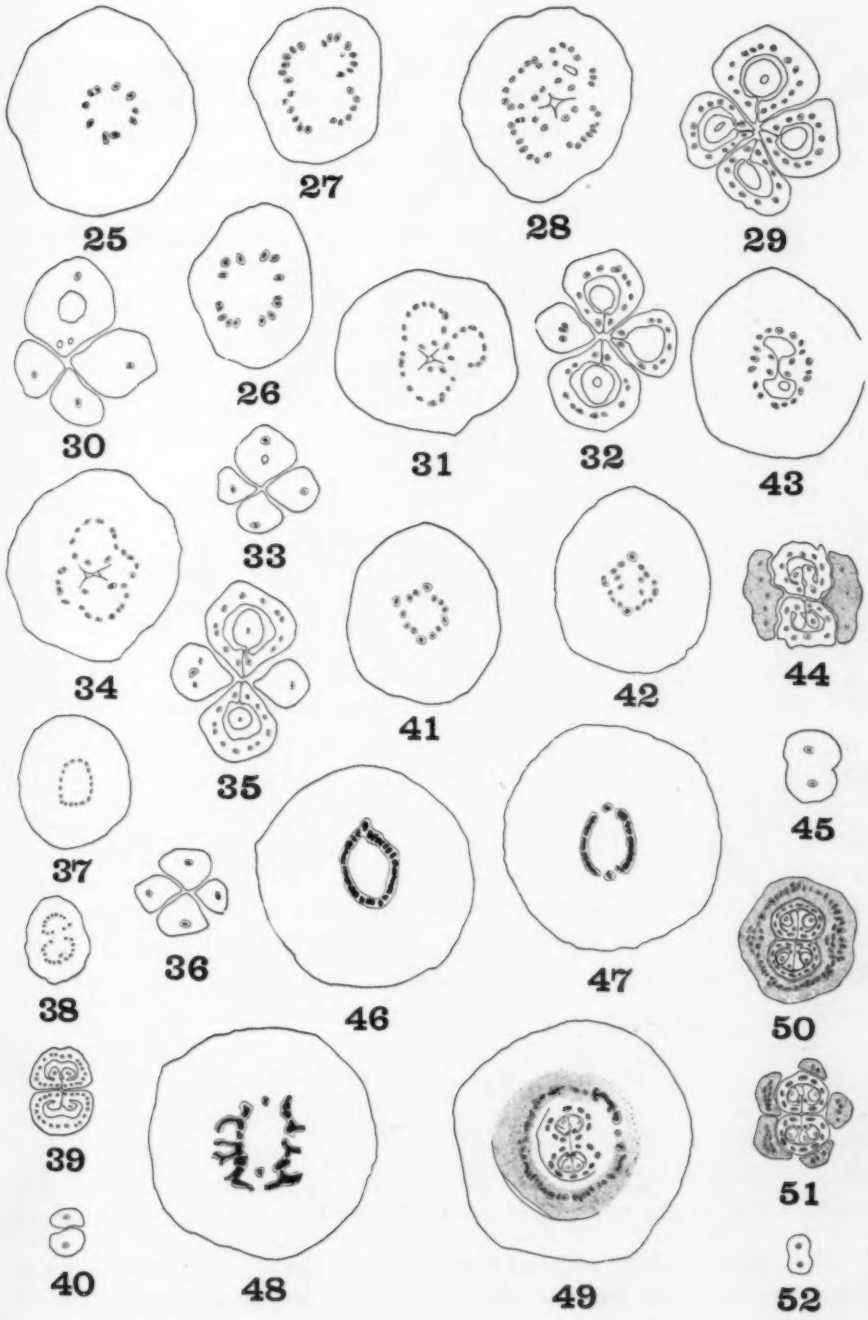
Although predominantly bicarpellary, the Apocynaceae include a few polycarpellary genera constituting the tribe Pleiocarpeae of the subfamily Plumerioideae. The number of carpels in this tribe varies from two to five, the whole range being encountered amongst different species of the single African genus *Pleiocarpa* (fig. 7). In some species of *Pleiocarpa* the number of fertile carpels tends to vary, as will be shown presently. The ovary of all polycarpellary genera always is apocarpous, but the component carpels are united by a rather poorly organized style within which the number of vascular bundles corresponds (cf. figs. 29, 33).

Surrounding the ovary of Apocynaceae one usually finds a cycle of fleshy bodies known as "nectaries" or "disc lobes." The nectaries frequently are separate, and two to five in number (figs. 3, 5), but occasionally they cohere to form a nearly uniform, annular structure (figs. 1, 2, 6). Occasionally the nectaries are quite as massive as the carpels, which they simulate in general aspect save for the fact that they do not contribute to the style (figs. 3, 8).

That the nectaries definitely are appendages and not merely meaningless hypertrophies of the receptacle is demonstrated by the fact that they contain definite vascular tissue associated with that of the gynoecium proper. The fundamental tissue comprises an elaborate assortment of secretory and storage cells a comprehensive discussion of which is without the scope of this paper (cf. pl. 3, figs. 6, 7; pl. 5, fig. 3). After a study of the floral anatomy of *Apocynum*, Woodson (1930) concluded that the nectaries of Apocynaceae should be interpreted as carpellodes. That position may now be given support by a study of numerous additional genera, particularly the polycarpellary species *Pleiocarpa mutica*.

The vascular anatomy of the ovaries and associated nectaries of all genera and species studied during the present investigations may be treated by representative illustrations which follow.

Figs. 25–52. Vascular anatomy of the gynoecium of Apocynaceae, traces to the perianth and stamens omitted. Explanation in the text. Figs. 25–36, *Pleiocarpa mutica;* figs. 37–40, *P. bicarpellata;* figs. 41–45, *Lochnera rosea;* figs. 46–52, *Mandevilla subsagittata*. In these diagrams glandular tissue pertaining to the nectaries is stippled.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Pleiocarpa

It has been impossible to obtain fresh material of the interesting genus *Pleiocarpa*. The genus is relatively poor in herbarium representation as well. However, three flowers were removed from a herbarium specimen of *P. mutica* Benth., and prepared in serial sections after softening in "diaphanol" according to a method outlined in a previous account by the senior writer (Woodson, 1935). It is interesting to observe that these flowers constituted a cymule, the first flower to be observed being the central member.

Flower 1 (figs. 25–30 inclusive). After the departure of the perianth and stamen traces, the receptacular stele is found to consist of approximately 10 to 20 small bundles assuming a roughly circular orientation (fig. 25). Four adjacent pairs of these, situated at regular intervals within the stele, migrate toward the center, and are subsequently found to be the placental bundles of the four component carpels (figs. 26, 27). This interpretation shortly is proved by the appearance of ovary cavities and the subsequent separation of the carpels from the receptacle (figs. 28, 29). It is not until after the full organization of the carpels that the respective midribs become obviously distinct from the sessile secondary venation. In this flower all four carpels are hollow and fertile.[2]

Flower 2 (figs. 31–33 inclusive). After the departure of the perianth and staminal bundles, the residual receptacular stele consists as in the first flower of about 10–20 bundles arranged in a circle. Two pairs of these migrate toward the center, but the remaining two pairs observed in the previous flower are represented merely by a single bundle for each, which likewise migrate centripetally (fig. 31). It is not surprising, therefore, to find that subsequent events produce but three hollow carpels, only two of which, incidentally, are ovuliferous. The fourth carpel of the first flower is replaced by a solid carpellode (fig. 32). Both the sterile carpel and the solid carpellode contribute their midribs to the style, however, and can scarcely be considered as precisely equivalent to "nectaries" (fig. 33).

Flower 3 (figs. 34–36 inclusive). In this flower the residual stele of the receptacle consists, as before, of about 10–20 bundles. Four solitary, equidistant bundles migrate centripetally (fig. 34), and it is found subsequently that the ovary consists of two hollow, ovuliferous carpels alternating with two solid carpellodes which have been supplied by the arcs of bundles intervening between the pairs of placental traces (fig. 35). As in the second

[2] The use of the terms "hollow," "fertile," "sterile," and "solid" are used here strictly in a descriptive sense and without the specialized meanings of the writers on "carpel polymorphism" (Saunders, 1925).

flower, the carpellodes contribute their midribs to the style (fig. 36).

In the three flowers of a single cymule of *Pleiocarpa mutica*, therefore, a striking tendency to the reduction of the number of fertile carpels is found. In *P. bicarpellata* Stapf sections of several flowers have revealed but two (fertile) carpels in each case, and without any indication whatever of carpellody (cf. figs. 37–40 inclusive). The anatomy of these ovaries is essentially similar to that of *Cerbera Tanghin*, which will be explained subsequently.

Lochnera

The two ovuliferous carpels of several genera and species of Apocynaceae alternate with as many fleshy nectaries. A good illustration of this condition is *Lochnera rosea* (figs. 41–45 inclusive). In this species, as in *Pleiocarpa mutica*, the residual stele of the receptacle consists of about 20 bundles. As in the third flower of *P. mutica* also (fig. 34), four equidistant bundles migrate centripetally to produce the placental bundles of the two ovuliferous carpels; the two arcs of bundles intervening supply the two alternating nectaries (figs. 42–44). These true nectaries differ from the solid carpellodes observed in the third flower of *Pleiocarpa mutica* only in so far as they do not contribute to the style (fig. 45). Nevertheless the true nectaries of *Lochnera* and the solid carpellodes of *Pleiocarpa* are almost exactly similar as far as their vascular origin is concerned, and their position also argues in favor of their relationship.

It appears obvious that the nectaries of *Lochnera* should be considered as carpellodes, and this interpretation extends itself to other nectaries of Apocynaceae. Other species possessing two nectaries of an anatomical organization essentially similar to that of *Lochnera rosea* include:

Vinca major L.
V. minor L.

Mandevilla

The vascular organization of the ovary and nectaries of *Mandevilla subsagittata* (R. & P.) Woods. (figs. 46–52 inclusive) is representative of all investigated species of *Mandevilla* and several closely related genera. In this species the receptacular stele unites after the departure of the corolline and staminal traces, a rare phenomenon amongst the Apocynaceae that have been investigated (fig. 46). The stele is somewhat elliptical in section, and very shortly the midribs of the two carpels depart by gaps from the opposite, narrowed ends of the ellipse (fig. 47). Meanwhile, the two broad arcs of the stele branch outward into an aggregate of separate bundles (fig. 48). The stele is now completely disrupted into

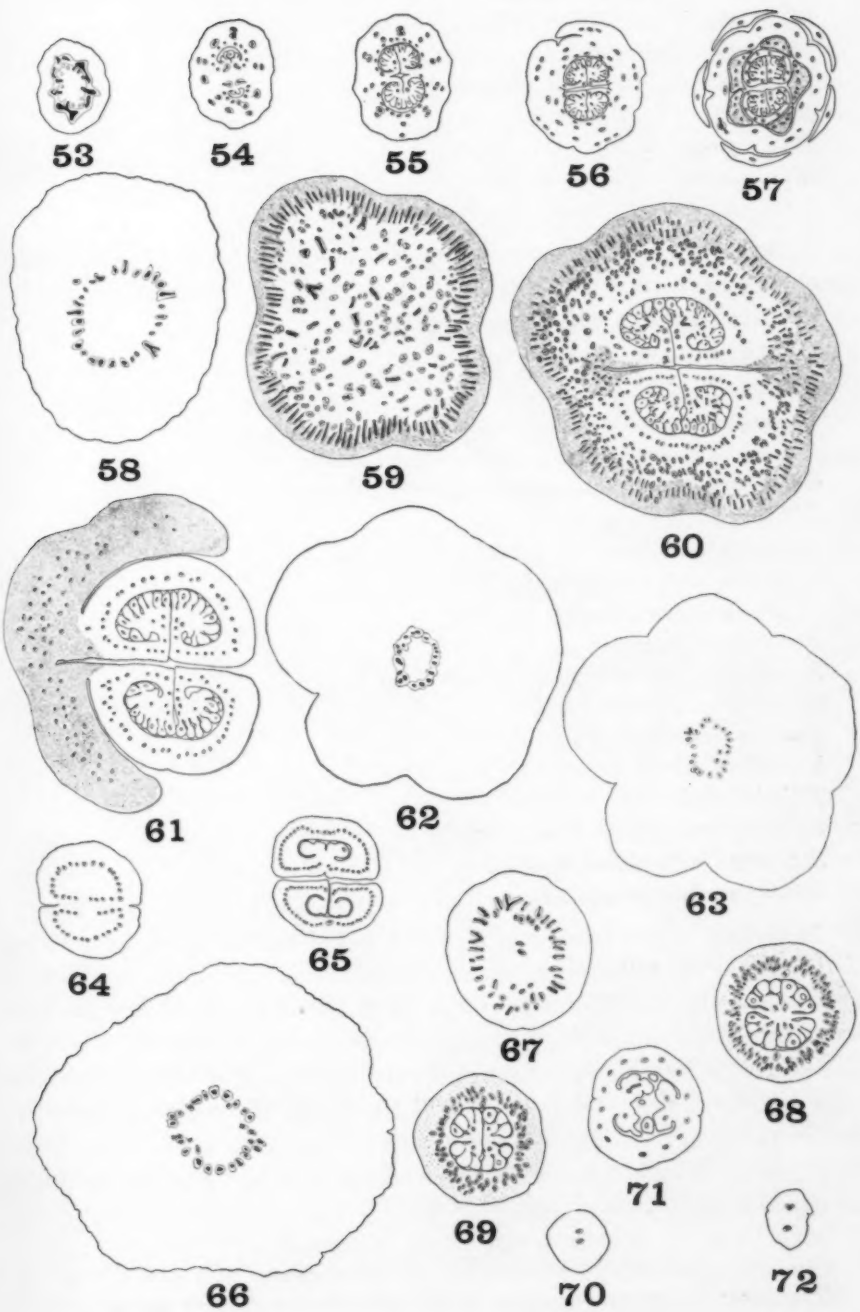
bundles of varying size, but all smaller than the two opposed midribs which have remained unbranched.

Centripetal migration of four to eight bundles roughly equidistant from the midribs now takes place to form the lateral bundles of each carpel. The organization of the carpels and the nectaries now takes place with the peripheral residual bundles supplying the latter (figs. 49, 50). The nectaries of this species, which superficially appear to be five in number in ordinary dissections, are found to be united at the base. Very shortly after their organization from the receptacle and the gynoecium proper, radial division of the bundles, occuring first in two planes alternate with the two carpels, produces something of a "polydesmic" condition, which is continued for a short space even after the organization of the five separate nectary lobes (figs. 50, 51).

The nectaries of *M. subsagittata* and its congeners, as well as those of other genera having this type of gynoecial anatomy, are usually five in number. But whether the gross aspect of the bodies should be taken as indicating the sterilization of five separate carpels, or whether the fact that the vascular supply of the cycle of nectaries has its origin in a somewhat similarly bilateral fashion to those of *Lochnera* is an indication that here also but two carpellodes are involved, is not wholly decided by the evidence, although the latter appears probable. Evidence to support the latter assumption may be found in the fact that only two nectary lobes are found in several species of *Mandevilla*, such as *M. splendens* (Hook). Woods., and *M. illustris* (Vell.) Woods. The 5-lobed condition in *M. subsagittata* and other species might be interpreted as an instance of ontogenetic schizogeny due to internal pressures within the developing pentamerous flowers. The annular nectary of several species of *Odontadenia*, such as *O. Hoffmannseggiana* (Steud.) Woods. is cleft into almost innumerable tooth-like segments whose number is certainly not indicative of the number of carpellodes actually involved.

In any event, the vascular supply of the nectaries of *M. subsagittata* differs from that of *Lochnera* chiefly in its adnation to the lateral bundles of the carpels; and the nectaries here as well are evidently to be considered as carpellodes. Other genera and species having a gynoecial skeleton similar to that of *M. subsagittata* include:

Figs. 53–72. Vascular anatomy of the gynoecium of Apocynaceae, traces to the perianth and stamens omitted save in figs. 53–57. Explanation in the text. Figs. 53–57, *Apocynum cannabinum;* figs. 58–61, *Stemmadenia Alfari;* figs. 62–65, *Cerebera Tanghin;* figs. 66–70, *Lacmellia edulis;* figs. 71–72, *Allamanda cathartica*. In these diagrams glandular tissue pertaining to the nectaries is stippled.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Macrosiphonia Brachysiphon (Torr.) Gray
M. Macrosiphon (Torr.) Heller
Mandevilla Bridgesii (Muell.-Arg.) Woods.
M. hirsuta (A. Rich.) K. Sch.
M. illustris (Vell.) Woods.
M. splendens (Hook.) Woods.
Mascarenhasia elastica K. Sch.
Mesechites trifida (Jacq.) Muell.-Arg.

Essentially the same vascular organization is found in numerous other species and genera, which differ chiefly in that the residual stele consists of separate bundles, rather than a siphonostele:

Allamanda cathartica L.
Forsteronia viridescens Blake
Lacmellia edulis Karst.
Malouetia guatemalensis (Muell.-Arg.) Standl.
Odontadenia Hoffmannseggiana (Steud.) Woods.
O. Schippii Woods.
Plumeriopsis Ahouai (L.) Rusby & Woods.
Prestonia acutifolia (Benth.) K. Sch.
P. portobellensis (Beurl.) Woods.
Rauwolfia tetraphylla L.
Rhabdadenia biflora (Jacq.) Muell.-Arg.
Thenardia Galeottiana Baill.
Thevetia peruviana (Pers.) K. Sch.
Trachelospermum difforme (Walt.) Gray
T. jasminoides (Lindl.) Lem.
Urechites Andrieuxii Muell.-Arg.
Zschokkea panamensis Woods.
Z. ramosissima Muell.-Arg.

In certain of the foregoing, repeated radial and tangential branching of the nectary bundles produces an elaborate "polydesmic" condition; in certain also the centripetal migration of the four placental bundles may occur before the branching outward of the nectary traces. In some, the four placental laterals may fuse into pairs composed of the adjacent laterals of either carpel, later dividing again before the complete organization of the ovary (cf. figs. 67–69 inclusive). But such variations may be encountered occasionally within flowers of a single species, and thus appear relatively insignificant.

Stemmadenia

The most elaborate and confusing system of vascular supply for the gynoecium is found in the investigated species of *Stemmadenia* and certain

more or less closely related genera. In *S. Alfari* (cf. figs. 58–61 inclusive), the departure of the corolline and staminal bundles leaves an elaborately dissected residual stele composed of many bundles uniseriately arranged in roughly circular outline (fig. 58). These commence an extended system of branching, both radially and tangentially, until the stele consists of innumerable strands occupying the receptacle in a manner almost "monocotyledonous" (fig. 59).

At no time are the midribs and placental laterals distinguishable as such. Nevertheless a definitely glandular development of the outermost tissue strongly suggests the adnation of an annular nectary to which the outermost vascular bundles probably are referable.

The scattered bundles merely crowd away to allow the formation of the carpellary cavities; after which those which are to supply the carpels are definable by forming an invaginated arc about the two cavities. The bundles other than this single series proceed up into the nectaries, which remain adnate to the ovary save very shortly at the upper margins (figs. 60, 61). "Polydesmy" therefore frequently is characteristic of the nectaries, and never of the carpels proper.

Other species having a gynoecial anatomy similar in general to that of *S. Alfari* include:

Funtumia elastica (Preuss.) Stapf
Stemmadenia grandiflora (Jacq.) Miers
S. obovata (Hook. & Arn.) K. Sch.
Tabernaemontana acutissima Muell.-Arg.
T. arborea Rose
T. chrysocarpa Blake
T. Cumingiana A.DC.
T. divaricata R.Br.

Cerbera

The vascular anatomy of apocynaceous ovaries which are unaccompanied by nectaries shows great uniformity. That of *Cerbera Tanghin* Hook. (figs. 62–65 inclusive) may illustrate this group. After the departure of the corolline and staminal traces the receptacular stele is seen to constitute a hollow cylinder consisting of several distinct bundles, or rarely a poorly organized siphonostele which soon becomes dissected (fig. 62). At this stage the midribs ordinarily are not obvious as such.

Soon, however, the number of bundles increases by tangential branching, and the stele thus increased undergoes a furrowing in two opposed positions to form the vascular supply of the respective carpels (figs. 63, 64), the cavities of which shortly make their appearance. By this time

the carpels are organized fully, and the midribs usually are somewhat larger than the lateral veins, but never is this difference very pronounced (fig. 65). As appears to be invariable in the Apocynaceae, the midribs proceed into the common style, the lateral traces disintegrating distally. Other genera and species which are destitute of gynoecial nectaries and show an ovarian anatomy similar to that of *C. Tanghin* include:

Adenium coetenium Stapf
Amsonia ciliata Walt.
Cycladenia humilis Benth.
Haplophyton cimicidum A.DC.
Nerium Oleander L.
Pleiocarpa bicarpellata Stapf
Plumeria rubra L.
Rhazya orientalis (Dcne.) A.DC.
Strophanthus dichotomus A.DC.
S. gratus A.DC.
S. sarmentosus A.DC.

Although the foregoing appear superficially to be destitute of a nectary about the ovary, and no vascular tissue to supply such an organ exists, several genera (cf. *Cycladenia*) possess carpels which are united for a short distance at the very base, where a rather poorly defined glandular development of the superficial tissues occurs.

Apocynum

The vascular anatomy of the gynoecium of *Apocynum* and *Trachomitum*, both members of the small subfamily *Apocynoideae*, differs so markedly from that of other members of the Apocynaceae, and is so closely involved with the vascular skeleton of the other components of the flower, that it appears necessary to present a condensed account of the anatomy of an entire, representative flower (cf. figs. 53–57 inclusive).

The stele of *Apocynum cannabinum* is rather irregularly 10-lobed in the lower receptacle (fig. 53). Of the ten, alternate lobes depart to provide the midribs of the five calyx and corolla members, and from each the respective laterals are produced according to the Type III calyx plan. As the perianth midribs depart they leave in their wake a rather indefinite number of small, poorly defined bundles to constitute the residual stele. Two opposed pairs of these bundles migrate toward the center of the stele to form the placental bundles of the two carpels in a manner similar to that observed for *Pleiocarpa*, *Cerbera*, and other genera. The residual stele remaining after the departure of the perianth traces, therefore, is devoted solely to the vascular supply of the two carpels.

Subsequent to their departure from the receptacular stele, however, it is found that the ten "perianth traces" are really compound structures. For the five staminal traces prove to be adnate to the calycine midribs; and, furthermore, *the corolline midribs are found to be adnate to the five bundles which supply the five gynoecial nectaries* (figs. 54–57) inclusive. The five nectary midribs, upon becoming free from the corolline midribs, branch tangentially to produce a somewhat variable number (usually two) of laterals. Full tissue differentiation of the calyx, corolla (with the epipetalous staminal filaments), nectaries, and carpels is obtained at about this time.

This curious adnation of the staminal to the calycine traces, and of the nectary to the corolla traces, has been observed only amongst the following genera and species, all of which are referable to the subfamily Apocynoideae:

Apocynum androsaemifolium L.
A. cannabinum L.
Trachomitum venetum (L.) Woods.

The most striking and significant feature of this type of gynoecial skeleton is found in the fact that the carpellary and nectary vascular supplies are quite independent, removing as well the possibility of interpreting the nectaries as merely "enlargements of the receptacle or torus," and of no evolutionary significance.

EVOLUTIONARY MODIFICATION OF THE GYNOECIUM

We have observed that in *Pleiocarpa mutica* there can be found in a single cymule an almost perfect transition from four fertile carpels to two fertile carpels and two alternate, solid carpellodes. It has also been pointed out that the two nectaries which alternate with the fertile carpels of *Lochnera* and *Vinca* differ from the solid carpellodes of *Pleiocarpa* only in the fact that they do not contribute to the style. The "nectaries" certainly appear to be equivalent to the "carpellodes" both from the observed variation in *Pleiocarpa* and from the standpoint of comparative vascular anatomy. If the interpretation of the gynoecial nectaries as carpellodes be accepted, phylogenetic significance will be given to the diversity of modification amongst the nectaries, and to their various relationships to the ovary proper. A few Apocynaceae are polycarpellary at the present day; but the frequency of nectaries amongst the family as a whole would indicate polycarpy to have been the original condition probably throughout, or essentially so.

In many Apocynaceae the nectaries are completely free from the

ovary. But in others they are found to be adnate to the very base of the ovary. In certain genera and species the nectaries are adnate throughout their entire length, or free merely at their upper margins (cf. *Stemmadenia*, figs. 60, 61). When the adnation of an annular nectary is virtually complete, its presence may be determined superficially only by the somewhat enlarged, glandular base of the ovary (cf. pl. 5, fig. 4). When seen in transverse section, however, two more or less distinct vascular systems frequently are found, the outer pertaining to the adnate nectary, and the innermost to the carpels (cf. pl. 5, figs. 1, 2). That the cohesion and subsequent adnation of the cycle of nectaries may influence syncarpy of the ovary is indicated by the fact that in most syncarpous ovaries the presence of an adnate nectary cycle may be demonstrated, either by a glandular base of the ovary wall, or that together with a double vascular supply.

In some cases, as in *Cycladenia humilis*, the ovary may be syncarpous and bilocular for the basal half roughly, and apocarpous above. In such ovaries, although a second vascular system cannot be demonstrated, the syncarpous base is conspicuously glandular; and one easily assumes that although the nectary vascular supply has been eliminated the effects of adnation remain in the syncarpy and the glandular epidermis of the ovary base. It should be observed that this interpretation receives support from the fact that obviously simple, apocarpous ovaries of Apocynaceae never are provided with a glandular epidermis.

The peculiar adnation of the nectaries to the ovary of certain Apocynaceae recalls the current theory of "carpel polymorphism" (Saunders, 1925). And surely it appears that that theory should rest upon some such foundation as that found in Apocynaceae. But the observations which we have made necessitate no specious assumptions of "valve" and "solid" carpels, either "sterile" or "fertile," in confusing variety, the fallacy of which has been revealed so satisfactorily by Eames (1931). We wish to emphasize that our conception of the carpel is that of Eames and not of Saunders (1925). This may be effected most expeditiously, perhaps, by adding that Miss Saunders has expressed privately to the senior author that it is her conviction that the ovary of *Apocynum* consists of at least six carpels; two "sterile valves" plus four "fertile, solid carpels"; and that the nectaries are merely enlargements of the receptacle and of no particular significance.

DISCUSSION AND SUMMARY

Perhaps the chief interest in the floral morphology and anatomy of Apocynaceae is found in the interpretation of three categories of structure which are presumed to be vestigial:

(*1*). *The calycine squamellae* are small internal appendages at the base of the calyx lobes which are sufficiently constant in position, shape and number to form the basis of taxonomic differentiation of genera and species. These appendages usually are glandular and without vascular tissue. In a few genera, however, they are provided with small traces produced from the lateral veins of the calyx lobes. Therefore they are interpreted as stipular vestiges. Similar calycine appendages are found in certain other families of Gamopetalae. In one genus of Asclepiadaceae they have been construed as stipular in nature (Woodson, 1936) and future studies may lead to a similar interpretation in such families as Gentianaceae, Oleaceae, etc.

(*2*). *The corolline scales* likewise are internal appendages of the corolla which are of considerable taxonomic value. Where they are well developed these scales are found to have an interesting vascular anatomy, with the traces supplied as branches from the corolla lateral veins in a manner very similar to that found in many vegetative stipules such as those of *Pelargonium*. The corolline scales therefore also are interpreted as stipules. Various "coronas" and "scales" are found upon the petals of many flowering plants, such as Caryophyllaceae, Gentianaceae, Asclepiadaceae, etc. Subsequent investigations may well reveal these, also, as stipular vestiges and the corolline members as essentially foliar in nature.

(*3*). *The gynoecial nectaries* constitute a cycle of two to five more or less fleshy, ovoid bodies about the base of the ovary. Occasionally the nectaries cohere to form an annular structure. Previous studies by the senior author (Woodson, 1930) had shown the vascular organization of these structures to be rather similar to that of the fertile carpels. In the present investigations an almost perfect transition from four fertile carpels to two fertile carpels and two alternate solid carpellodes has been demonstrated to occur in a single cymule of *Pleiocarpa mutica*. The nectaries of other Apocynaceae, such as *Vinca* and *Lochnera*, differ from the carpellodes of *Pleiocarpa* essentially only in the fact that they do not contribute to the style. Hence the interpretation of the nectaries as carpellodes finds additional support.

In some genera a peculiar condition is found in which the nectaries cohere mutually and become adnate to the functional ovary, giving rise to a phenomenon which the writers wish to emphasize as not coinciding with the theory of "carpel polymorphism." Apocynaceous ovaries of several genera which appear to be simple from ordinary dissections are found to bear rather obscure traces of such nectarian adnation.

The interpretation of the nectaries as constituting a cycle of carpellodes apparently would indicate the derivation of Apocynaceae from poly-

carpellary ancestors; and the presence of stipular vestiges in the calyx and corolla, as well as at the vegetative node, might indicate a phylogenetic relationship with the extant order Rosales. Similar gynoecial nectaries occur in other families of Angiospermae such as Caryophyllaceae, Primulaceae, Gentianaceae, Convolvulaceae, Solanaceae, Caprifoliaceae, etc. and probably would repay similar study. The hypogynous "disc" of *Mertensia* (Boraginaceae) recently has been interpreted as of carpellode origin by the junior author (Moore, 1936).

The vascular anatomy of the calyx is found to be of interest in that there is an apparent transition from the 3-trace unilocular to the 1-trace condition of the lobes. Although four general types of organization are encountered predominantly, an almost bewildering variation occurs, occasionally amongst flowers of a single inflorescence.

Although we believe that contributions of some value have been made to the phylogeny of Apocynaceae through our investigations, it must be granted that the results appear to be of little value to pure taxonomy. The vascular systems of the calyx, for example, do not coincide in general with existing classifications, and neither do they support the erection of a more satisfactory system. It probably should be assumed that the present systematic divisions of the family, which appear fairly natural upon their basis of gross morphology, are of great antiquity and have undergone parallel evolution of a certain degree.

MISSOURI BOTANICAL GARDEN,
WASHINGTON UNIVERSITY,
SAINT LOUIS, MO.

HURON COLLEGE,
HURON, S. D.

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Explanation of plates

(All photomicrographs from transverse sections unless otherwise stated)

PLATE 3

Fig. 1. Pedicel of *Rauwolfia tetraphylla* L., showing invasion of the pith by strands of internal phloem. (×45)

Fig. 2. Same as fig. 1, showing tracheid of protoxylem (*t*) differentiated within a medullary strand of internal phloem. (×230)

Fig. 3. Vegetative node of *Mandevilla Bridgesii* (Muell.-Arg.) Woods., showing origin of interpetiolar stipular appendages. (×16)

Fig. 4. Flower of *Mesechites trifida* (Jacq.) Muell.-Arg., general morphology: *ca*—calyx tube; *co*—corolla tube; *sq*—squamellae; *n*—nectaries; *o*—ovary. (×12)

Fig. 5. Vegetative node of *Prestonia acutifolia* (Benth.) K. Sch., showing origin of intrapetiolar stipular appendages. (×16)

Fig. 6. Flower of *Vinca minor* L., showing carpels and alternate nectaries. (×28)

Fig. 7. Sector of flower of *Mandevilla subsagittata* (R. & P.) Woods., longitudinal section, showing nectary (*n*) and squamella (*sq*). (×28)

PLATE 4

Fig. 1. Sector of flower of *Mesechites trifida* (Jacq.) Muell.-Arg., showing marginal origin of squamellae (*sq*) (×50)

Fig. 2. Sector of flower of *Mandevilla Bridgesii* (Muell.-Arg.) Woods., showing squamellae (*sq*). (×50)

Figs. 3–4. Sector of flower of *Mandeville subsagittata* (R. & P.) Woods., showing marginal origin of "opposite" squamellae. (×50)

Fig. 5. Sector of flower of *Funtumia elastica* (Preuss) Stapf, showing migration of squamella traces (*st*) from the calyx. (×50)

Fig. 6. Squamella of *Strophanthus gratus* A. DC. showing bicollateral trace (*st*) derived from calyx. (×210)

PLATE 5

Fig. 1. Ovary of *Zschokkea panamensis* Woods. showing adnation of the annular nectary. The vascular systems of the nectary (*nt*) and the ovary proper (*ot*) remain distinct. The ovary is syncarpous but bilocular with axile placentation. (×17)

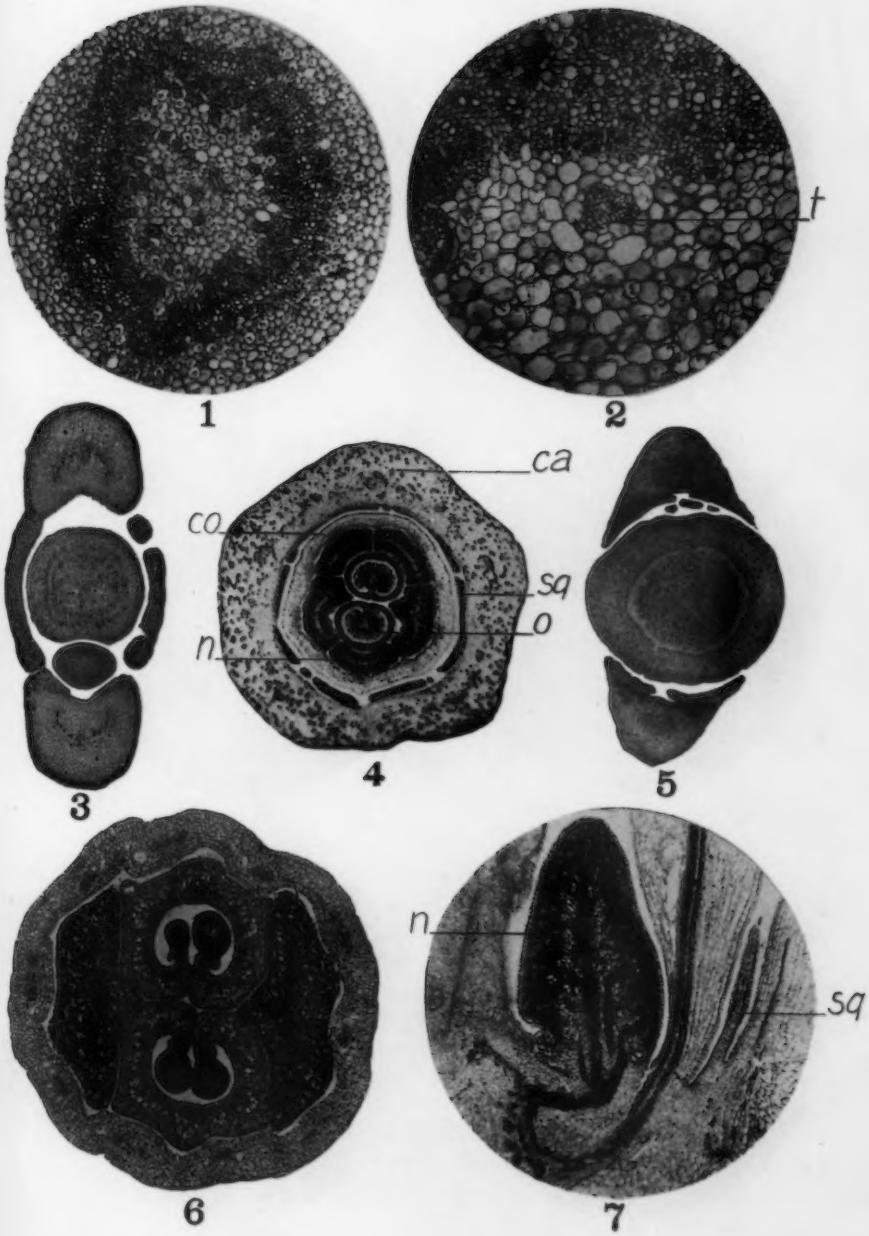
Fig. 2. Ovary of *Lacmellia edulis* Karst. showing adnation of the annular nectary. The vascular systems of the nectary (*nt*) and the ovary proper (*ot*) remain distinct. The ovary is syncarpous and unilocular with parietal placentation. (×17)

Fig. 3. Sector of flower of *Mandevilla subsagittata* (R. & P.) Woods., showing annular base of the nectaries which are free from the carpels which they surround. (×20)

Fig. 4. Sector of flower of *Tabernaemontana chrysocarpa* Blake, longitudinal section, showing adnation of the annular nectary (*n*). (×25)

Fig. 5. Sector of flower of *Plumeria rubra* L., longitudinal section, showing the almost completely inferior ovary. (×25)

Fig. 6. Sector of flower of *Urechites Andrieuxii* Muell.-Arg., longitudinal section, general morphology: *ca*—calyx; *sq*—squamella; *co*—corolla; *a*—anther; *s*—stigma; *o*—ovary; *n*—nectary. (×25)



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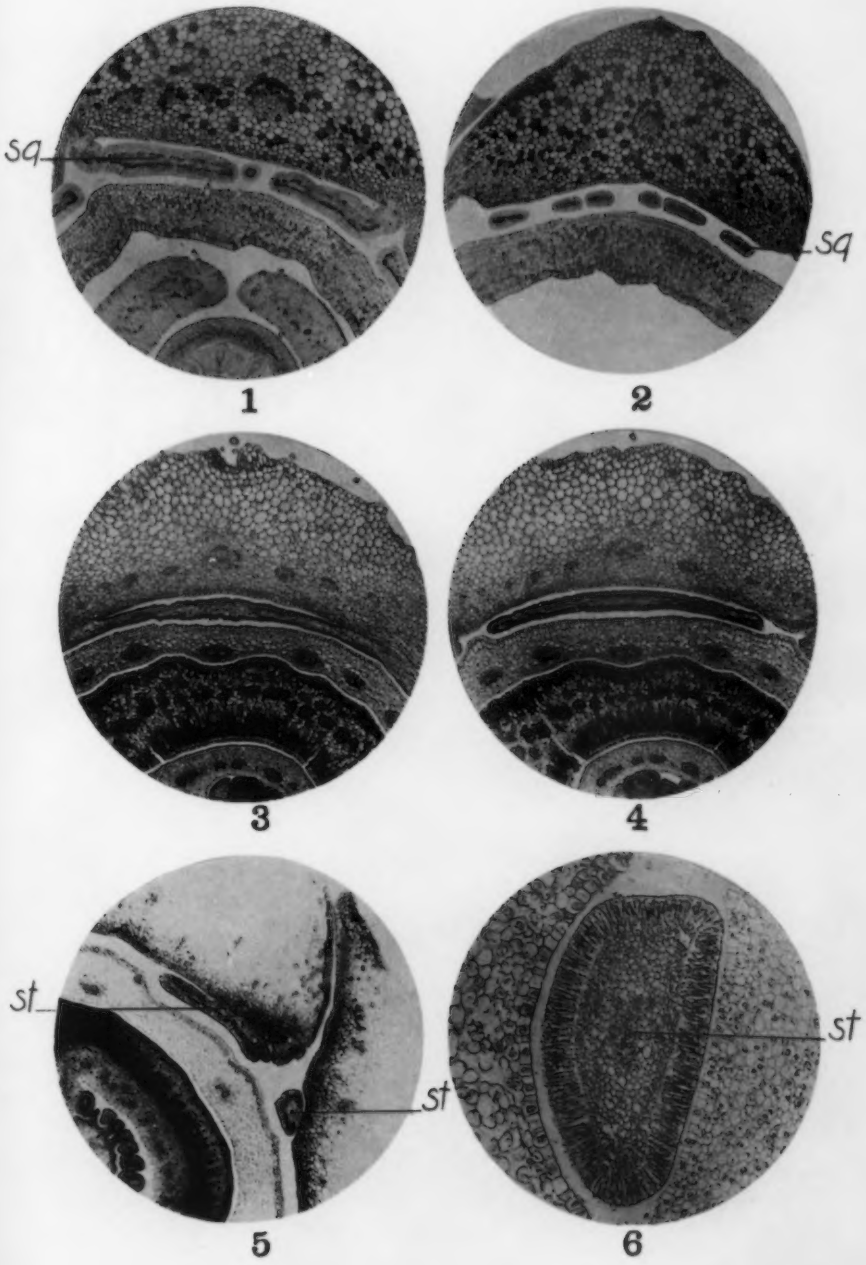

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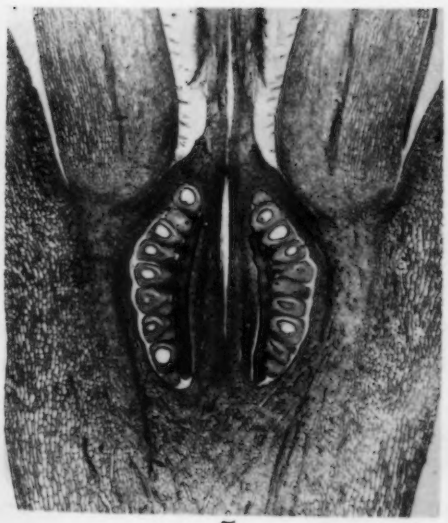

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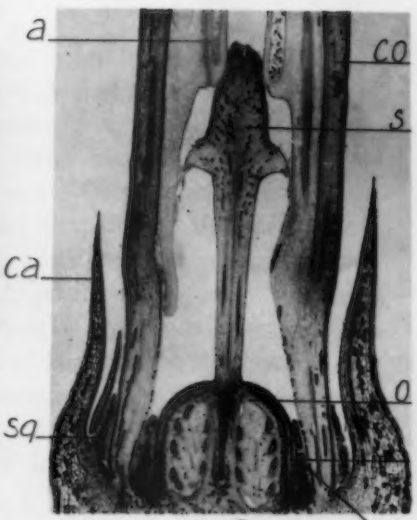

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Notes on fungi from the lower Mississippi Valley[1]

L. O. Overholts
(with figures 1–13)

From July until October of 1931 the writer was in the employ of the office of Forest Pathology of the United States Department of Agriculture. Most of this period was spent in a reconnaissance survey of timber decays and their causal fungi as they occur in the hardwood forests of the lower Mississippi Valley. Most of the time was spent in northeastern Louisiana in the region adjacent to the towns of Lake Providence and Ferriday, from which points excursions were made into adjacent Arkansas and Mississippi. About 500 collections of fungi, representing approximately 200 species, mainly of wood-inhabiting forms, were made and subsequently determined. These form the basis of the present report.

In the course of these investigations the writer was accompanied at times by members of the Forest Pathology division of the Southern Forest Experiment Station at New Orleans, and throughout the summer by Mr. Frank Kaufert without whose assistance the list would be much less complete. In the identifications I have had also considerable assistance from Mr. Ross W. Davidson of the Washington Office of Forest Pathology. Dr. C. L. Shear and Miss Edith K. Cash have made some identifications of collections falling into their special fields. Several collections of resupinate Hymenomycetes still remain to be determined, but it is impossible, because of the existing chaos in the genera to which they belong, to complete them at this time.

The generally dry atmospheric conditions which had prevailed during the preceding two years was both an advantage and a handicap; the former because it enabled us to penetrate swamp lands that normally are more inundated and inaccessible, and the latter because of its probable effect in reducing the number of species and collections obtained. This last item was in part overcome by the fact that during the summer of 1931 itself, rains, though not always heavy, were frequent enough during July and August to produce at least a fair crop of sporophores.

Viewed against a background of collecting in the wooded areas of the Allegheny Mountains the bottom hard-wood lands along the lower Mississippi River present some interesting contrasts. In the *Polyporaceae* there is the usual abundance of sap-wood inhabiting species, and the usual paucity of sporophores of heart-wood decaying species, or if sporo-

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phores of the latter group are slightly more abundant it may be due to the presence of certain species inclined to fruit more prolifically, and seldom found in the Allegheny region. But in other families the differences are more striking, if one may consider the summer of 1931 as approaching normality. One is particularly impressed by the lack of both individuals and species in the families Agaricaceae, Boletaceae, and Clavariaceae. While little attempt was made to collect specimens in these groups except for wood-inhabiting Agaricaceae, very few species were encountered. The Russulae and Lactariae that occur so abundantly in favorable seasons in the Allegheny region seem rare indeed, and terrestrial species of other genera were rarely seen. A single bolete, *Boletus chrysenteron* was common enough, but few others were seen. In the Clavariaceae not a single specimen was observed. Terrestrial Hydnaceae were likewise absent. In the Thelephoraceae, the wood-inhabiting species seemed fairly common, but here again terrestrial forms were rare.

In the Polyporaceae new information has been obtained on a considerable number of species. The status of *Polyporus ludovicianus*, a little known species, has been cleared up, and the species shown to be of great importance in causing an extensive butt-rot in Quercus and Liquidambar. It fruited abundantly and it is surprising that it has so long remained obscure. *P. fissilis* was collected in abundance and likewise proved to be highly important in the pathology of both Quercus and Liquidambar. An extensive and highly characteristic large pocket rot of Quercus is now rather definitely attributed to *P. zonalis* although some further study of that species is highly desirable in the light of the fact that essentially the same rot occurs in much more northward stations, apparently attributable to either or both *Poria undata* and *Polyporus rigidus*, all of which, however, have sporophores that are very similar in their essential characters. *P. sulphureus* seems to be just as ubiquitous in Louisiana as in more northern regions, while *P. dryophilus* and *P. dryadeus*, long known for their heart-rotting propensities in northern oaks, are strangely uncommon or occur not at all in this region. *P. lucidus* has been shown to be the cause of extensive heart decays in living Quercus, and this information came as a considerable surprise. *P. hispidus* is common on living Quercus and likewise causes an extensive and rather important decay, and as seems to be true in the north, is usually associated with the occurrence of conspicuous elongated wounds or cankers. *P. palustris* seems to cause an extensive brown heart-rot in living pine, and this relationship has not previously been reported. The same is true for *Fomes Calkinsii*, or its near relative *F. robustus*, on Quercus, but the species is probably not so

important. No additional information was secured as to the cause of "pecky cypress" but it is a safe assumption that it is not caused by *Fomes geotropus* as has been stated.

Owing to the fact that the relatively small amount of collecting that has previously been done in this region has not emphasized the pathological aspects of the situation, much new information has been secured as to generic substrates of numerous species of timber-inhabiting fungi. Most of this, together with additional notes, will be presented with each species.

Specimens of a considerable number of the species collected are deposited at the Southern Forest Experiment Station in New Orleans. A larger and nearly complete representation of species has been deposited in the office of Forest Pathology at Washington. A nearly complete representation of both species and collections is in the writer's herbarium, while certain duplicates have been filed in the herbarium of the Pennsylvania State College.

While considerable collecting was done in each of the states of Louisiana, Mississippi, and Arkansas, the species listed are to be regarded as originating in Louisiana unless otherwise specified by state abbreviations.

ASCOMYCETES

Bolinia tubulina (A. & S.) Sacc. on Gleditsia. *Cenangella Ravenelii* (Berk.) Shear on Ilex. *Daldinia concentrica* (Bolt.) Ces. & deNot. on Diospyros. *Dothichloe atramentosa* (Berk. & Curt.) Atk. on *Sporobolus Berteroanus*. *Hypocrea rufa* (Pers.) Fr. on Quercus; *H. sulphurea* (Schw.) Sacc. on Liquidambar. *Hypoxylon atropunctatum* (Schw.) Cooke on Fagus; *H. botrys* Ell. & Ev.; *H. haematostromum* Mont.? on Fraxinus; *H. rubiginosum* (Pers.) Fr. *Lachnum virgineum* (Batsch) Karst.? on Taxodium. *Nectria sanguinea* (Bolt.) Fr. on Liquidambar. *Nummularia clypeus* (Schw.) Cooke. *Phyllachora graminis* (Pers.) Fuckel on Panicum. *Rhytisma acerinum* (Pers.) Fr. on *Acer rubrum; R. Vaccinii* (Schw.) Aut. Am. on *Vaccinium arboreum* (La., Miss.). *Taphrina caerulescens* (Mont. & Desm.) Tul. on *Quercus nigra*.

FUNGI IMPERFECTI

Cercospora rhoina Cooke & Ellis on Rhus (Miss.). *Darluca filum* (Biv.) Cast. on *Melampsora Medusae* on *Populus deltoides* (La.) and on *Uromyces Lespedezae-procumbentis* on *Lespedeza repens* (Miss.). *Dendrochium compressum* Ell. & Ev. *Dendrostilbella* sp. on Celtis. *Endothiella gyrosa* Sacc. on Quercus. *Phyllosticta acericola* Ell. & Ev. on *Acer rubrum; P. Labruscae* Thuem. on Vitis. *Septoria Rubi var. pallida* Ell. & Holw. on Rubus.

BASIDIOMYCETES

ORDER I. USTILAGINALES

Entyloma australe Speg. on Physalis. (Ark.)

ORDER II. UREDINALES

Coleosporium Solidaginis (Schw.) Thuem. on Solidago; *C. Vernoniae* Berk. & Curt. on Vernonia. *Gymnosporangium germinale* (Schw.) Kern on Pyrus (Miss.). *Melampsora Humboldtiana* Speg. on Salix; *M. Medusae* Thuem. on *Populus deltoides*. *Phakopsora Crotonis* (Burr.) Arth. on *Croton capitatum*. *Puccinia Hydrocotyles* (Link) Cooke on Hydrocotyle; *Puccinia Polygoni-amphibii* Pers. on Polygonum; *P. Smilacis* Schw. on Smilax; *P. Xanthii* on Xanthium (Miss.). *Uromyces Lespedezae-procumbentis* (Schw.) Curt. on *Lespedeza repens* (Miss.); *U. Toxicodendri* Berk. &. Rav. on *Rhus Toxicodendron*.

ORDER III. HYMENOMYCETALES

FAMILY AURICULARIACEAE

Auricularia Auricula-Judae (Fr.) Schroet. on Celtis, Gleditsia, Liquidambar and Quercus; common, with some specimens as much as 25 cm. broad (La., Ark.); *A. rosea* Burt. *Septobasidium pseudopedicellatum* Burt on Crataegus; *S. retiforme* (Berk. & Curt.) Pat. on Quercus.

FAMILY TREMELLACEAE

Eichleriella Leveilliana (Berk. &. Curt.) Mont. on Crataegus. *Exidia alba* (Lloyd) Burt. *Sebacina incrustans* (Pers.) Tul. on dead Vitis and at bases of living Cornus and other shrubs. *Tremellodendron pallidum* (Schw.) Burt.

FAMILY DACROMYCETACEAE

Calocera cornea (Batsch) Fries on Gleditisa. *Ceracea corticioides* Ellis on Taxodium. *Guepinia spathularia* (Schw.) Fr. on Liquidambar and Taxodium.

FAMILY THELEPHORACEAE

Aleurodiscus acerinus (Pers.) Hoeh. & Lit. on Quercus. *Asterostroma cervicolor* (Berk. & Curt.) Massee on Planera, Quercus, and other hardwoods. *Coniophora olivascens* (Berk. & Curt.) Massee on *Populus deltoides*. *Corticium chrysocreas* (=*Odontia Archeri*); *C. galactinum* (Fr.) Burt on *Pinus taeda; C. lactescens* Burt? on Celtis; *C. lividum* Pers. on Quercus (La., Ark.); *C. portentosum* Berk. & Curt. on Gleditsia; *C. stramineum* Bres. *Hymenochaete Curtisii* (Berk.) Morg. on *Quercus marylandica; H. epichlora* (Berk. & Curt.) Cooke. *Peniophora carnea* (Berk. & Curt.) Cooke on Celtis;

P. cremea Bres. on Crataegus; *P. gigantea* (Fr.) Massee on Pinus; *P. Roumeguerii* Bres. on *Acer rubrum*, Carya, Crataegus, Diospyros, Quercus (La., Ark.). *Stereum fasciatum* Schw. on Quercus (La., Miss.); *S. frustulosum* Pers. on Quercus; S. *fuscum* (Schrad.) Quel. on Acer, Celtis, Fraxinus Quercus, and Ulmus (La., Ark.); *S. gausapatum* Fr. on Quercus (Ark.); *S. pargamenum* Berk. & Curt. (Fig. 4); S. rameale (Schw.) Fr. on Cephalanthus, Quercus (La., Ark.); *S. Ravenelii* Berk. & Curt.; *S. subpileatum* Berk. & Curt. on Liquidambar and Quercus (La., Ark.); *S. umbrinum* Berk. & Curt.

FAMILY HYDNACEAE

Hydnum ochraceum (Pers.) Fr. on Liquidambar, Nyssa, Quercus (La., Miss.); *H. pulcherrimum* Berk. & Curt. on Liquidambar and Quercus (La., Ark.). *Irpex cinnamomeus* on Quercus; *I. mollis* Berk. & Curt. on Liquidambar, *I. Ravenelii* Berk. on Quercus. *Odontia barba-Jovis* Fries; *O. brunnescens* n. sp. on Liquidambar; *O. ciliolata* (B. & C.) Miller; *O. farinacea* (Pers.) Bres; *O. fimbriata* (Pers.) Fr.; *O. macrodon* (Pers.) Bourd. & Galz.; *O. setigera* (Fr.) Miller on Liquidambar, Planera, Ulmus. *Radulum vinosum* n. sp.

Of the above species the following are worthy of further comment:

Hydnum pulcherrimum was one of the commonest fungi encountered. It is a sessile, white, soft species growing on logs and stumps or on wounded areas of living trees and specimens up to 15 cm. broad. Fresh specimens have a milky juice that becomes very sticky as it dries (fig. 2).

Odontia brunnescens n. sp. Resupinate, effused, membranous or subceraceous, with a thin pruinose-agglutinated margin of pale cream color; hymenium not cracked, cream-buff to clay color or pale cinnamon (Ridgway) when dry, thickly set with dome-shaped or slightly elongate protuberances that are separate or slightly confluent, projecting 80–250μ above the surface, broad and obtuse, barely visible to the unaided eye; in section with a slightly yellowish subiculum 60–80μ thick, composed of a narrow and scarcely discernible substratal layer of horizontal hyphae from which arises a broader and very compact central region of sub-erect hyphae with a narrow incrusted layer along its lower edge and sometimes with some incrustation above, bearing the basidial layer; cystidia of two types, one projecting on the granules and between them, with sub-bulbous base and tapering and sharp-pointed apex, 4–6 μ diameter below and there rarely slightly incrusted, the other especially abundant in the granules, imbedded or reaching the level of the basidial layer, never conspicuous, incrusted, hyaline, 35–40$\times$9–10μ; spore short-cylindric, smooth, hyaline, 4–6$\times$2–3μ.

On dead branch of Liquidambar. Type collected at Oak Grove, La., Aug. 17, 1931. (U.S.F.P. Herb. 50225; Overholts Herb. 15252) (figs. 1, 3).

The granules on the hymenial surface are broader than in most species of *Odontia*, but the presence of cystidia precludes reference of the plant to the genus *Grandimia*.

Odontia fimbriata (Pers.) Fries. On dead wood. Wildsville, La.

Radulum vinosum n. sp. Resupinate, effused for several centimeters, thin and adnate, without definite margin; hymenium with rather blunt teeth that are isolated or closely associated, up to 1 mm. long and 150–300μ diameter, everywhere vinaceous-drab or fawn color on drying; in section showing a distinct subiculum 200–300μ thick, composed of somewhat gelatinized and very densely arranged hyphae throughout, those toward the substratum subhorizontal and those toward the hymenium sub-erect, no incrustation, apparently about 3–4μ diameter and without cross-walls or clamps though too strongly gelatinized and agglutinated to be certain; basidia 2–3μ diameter; spores allantoid, bacilliform, smooth, hyaline, 3–4$\times$1μ; cystidia and gloeocystidia absent; crystals about 20μ diameter scattered through the subiculum and in the teeth.

On dead wood of deciduous trees. Type collected at Ferriday. La., Aug. 1, 1931. (U.S.F.P. Herb. 55624; Overholts Herb. 15254).

The gelatinized hyphae of the subiculum and their arrangement and compactness suggests rather the genus *Phlebia*, but the teeth are too well developed and too isolated to permit reference there. It is unfortunate that color records of the fresh plants were not obtained in the field, but the color on drying is distinctive.

FAMILY AGARICACEAE

Agaricus abruptibulbus Peck. *Cantharellus cibarius* Fr. *Clitocybe decora* Fr. on Taxodium. *Flammula eccentrica* Peck. *Hypholoma incertum* Peck. *Lactarius lactifluus* (L.) Fr. (La., Ark.); *L. subvellereus* Peck. *Lentinus tigrinus* (Bull.) Fr. *Lepiota Morgani* Peck; *L. procera* (Scop.) Fr. *Marasmius iocephalus* (Berk. & Curt.) Penn.; *M. siccus* (Batsch) Fr. *Omphalia campanella* (Batsch) Fr. *Panus angustatus* Berk. on Carya; *P. laevis* Berk. & Curt. on Liquidambar; *P. rudis* Fr. on Pinus and Quercus (La., Miss., Ark.); *P. stypticus* (Bull.) Fr. on Quercus. *Pleurotus corticatus* Fr. on Carya (Ark.); *P. ostreatus* (Jacq.) Fr. *Schizophyllum commune* Fr. on Carya, Diospyros, Gleditsia, Liquidambar (La., Ark.). *Volvaria bombycina* (Pers.) Fr. on *Acer rubrum* and Liquidambar.

Of the above species none were particularly abundant. *Lentinus tigrinus* was not collected but several wood rot isolations yielded cultures that produced typical sporophores of that species. *Lepiota Morgani* was fairly common in grassy woods and especially along grassy roadsides. *Marasmius iocephalus* was collected several times and is easily recognized

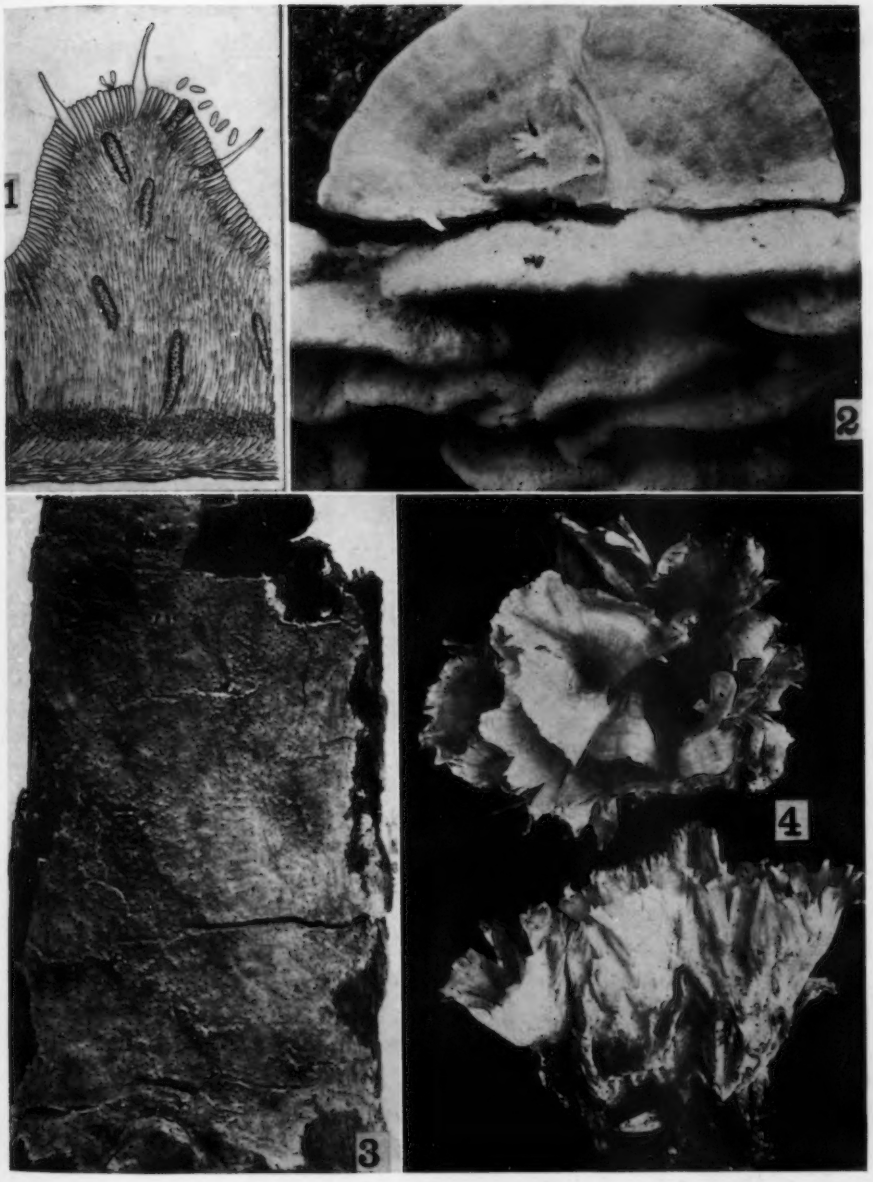

Fig. 1. Camera lucida drawing of section through a sporophore of *Odontia brunnescens*. Type collection. ×600.

Fig. 2. Photo of *Hydnum pulcherrimum*. Upper specimen showing hymenial surface. ×½.

Fig. 3. Photo of type material of *Odontia brunnescens*. ×2.

Fig. 4. Photo of fresh specimens of *Stereum pargamenum*. ×1.

by its violaceous color. *Panus laevis* was found several times growing from wounded areas in living trees of Liquidambar. It is likely to be mistaken for a *Pleurotus* but the pileus and stem are both very hairy and the sporophore assumes a uniform yellow color on drying. *Volvaria bombycina* was found several times growing from knots in living trees.

FAMILY BOLETACEAE

Boletus chrysenteron (Bull.) Fr. *Strobilomyces strobilaceus* Berk.

FAMILY POLYPORACEAE

Daedalea ambigua Berk. on Carya, Celtis, Diospyros, Gleditsia, Quercus (La., Miss., Ark.); *D. confragosa* (Bolt.) Fr. on Liquidambar and Quercus; *D. elegans* (Spreng.) Fr. on Carya and Gleditsia; *D. farinacea* (Fr.) comb. nov. (*Irpex farinaceus* Fr.) on Quercus; *D. unicolor* (Bull.) Fr. on Celtis. *Fomes applanatus* (Pers.) Gill. on *Populus deltoides; F. Calkinsii* (Murr.) Sacc. & Sacc. on Quercus; *F. conchatus* (Pers.) Gill. on Fraxinus; *F. densus* Lloyd on Carya and Fraxinus; *F. fraxineus* on Fraxinus; *F. geotropus* Cooke on Acer, Liquidambar, Magnolia, Populus, Ulmus (La., Miss.); *F. igniarius* var. *laevigatus* (Fr.) Overh. (*Poria laevigata* Fr.) on Fagus, Gleditsia, Quercus; *F. lobatus* (Schw.) Cooke on Quercus (La., Miss.); *F. marmoratus* (Berk. & Curt.) Cooke on Carya, Celtis, Diospyros Gleditsia, Liquidambar, Quercus, Ulmus; *F. Meliae* (Underw.) Murr. on Fraxinus, Gleditsia (La., Ark.); *F. rimosus* Berk. on Robinia; *F. tenuis* Karst; *F. torulosus* on Fraxinus (Ark.). *Lenzites betulina* (L.) Fr. on Liquidambar, Quercus (La., Ark.); *L. saepiaria* (Wulf.) Fr. on Pinus (La. Miss., Ark.). *Polyporus abietinus* (Dicks.) Fr. on pine slash (La., Miss.); *P. adustus* (Willd.) Fr. on Celtis, Gleditsia, Liquidambar, Quercus (La., Miss., Ark.); *P. anceps* Peck on *Pinus taeda* (Miss.); *P. arcularius* (Batsch) Fr. on Gleditsia; *P. biformis* (Kl.) Berk. on Carya and Quercus (La., Ark.); *P. cinnabarinus* (Jacq.) Fr. on Quercus (La., Ark.); *P. cristatus* (Pers.) Fr. (Ark.); *P. Curtisii* Berk. on Carya, Gleditsia, Quercus (La., Miss., Ark.); *P. cuticularis* (Bull.) Fr. on Acer, Celtis, Quercus, Ulmus (La., Ark.); *P. dichrous* Fr. on Carya, Cephalanthus, Fraxinus, Quercus, Ulmus (La., Ark.); *P. distortus* (Schw.) Fr. on Carya, Quercus (La., Ark.); *P. dryophilus* Berk. on Quercus; *P. fimbriatus* Fr.; *P. fissilis* Berk. on Liquidambar and Quercus; *P. focicolus* Berk. & Curt. (La., Miss.); *P. frondosus* (Dicks.) Fr. on Quercus; *P. galactinus* Berk. on Liquidambar and Quercus; *P. giganteus* on Quercus; *P. gilvus* (Schw.) Fr. on Cephalanthus, Crataegus, Diospyros, Fagus, Liquidambar, Pinus, Quercus, Taxodium (La., Miss., Ark.); *P. hirsutus* (Wulf.) Fr. on Celtis, Nyssa, Populus; *P. hispidus* on Quercus (La., Miss., Ark.); *P. hydnoides* (Sw.) Fr. on Carya,

Gleditsia, Liquidambar, Ulmus; *P. lucidus* (Curt.) Fr. on Celtis, Diospyros, Liquidambar, Planera, Quercus (fig. 9); *P. ludovicianus* (Pat.) Sacc. & Trott. on Liquidambar and Quercus (La., Ark.); *P. maximus* (Mont.) Overh. on Ulmus; *P. mutabilis* Berk. & Curt. on Diospyros, Nyssa, Quercus (La., Ark.); *P. nidulans* Fr. on Carya; *P. obtusus* Berk. on Quercus; *P. palustris* Berk. & Curt. on Pinus (La., Miss.); *P. pargamenus* Fr. on Fagus and Liquidambar (La., Ark.); *P. persicinus* Berk. & Curt.; *P. pinsitus* Fr. on Fraxinus and Gleditsia (La., Ark.); *P. porrectus* (Murr.) Sacc. & Trott.; *P. radiatus* var. *Cephalanthi* n. var. on *Cephalanthus occidentalis; P. rhipidium* Berk. on Liquidambar and Quercus (La., Ark.); *P. robiniophilus* (Murr.) Lloyd on Celtis (Miss.); *P. sanguineus* (L.) Fr. on Liquidambar and Quercus; *P. Schweinitzii* Fr. on Pinus; *P. sector* (Ehr.) Fr. on Carya, Liquidambar, Quercus (La., Ark.); *P. semipileatus* Peck; *P. Spraguei* Berk. & Curt. on Fraxinus, Liquidambar, Quercus (La., Ark.); *P. subectypus* (Murr.) Lloyd on Liquidambar; *P. submurinus* on Populus, Fraxinus, Quercus; *P. sulphureus* var. *cincinnatus* Morg. on Quercus; *P. supinus* (Sw.) Fr. on Carya, Diospyros, Fraxinus, Gleditsia, Liquidambar, Quercus, Ulmus; *P. tenuis* (Sacc.) comb. nov. (*Polystictus tenuis* Sacc.) on Taxodium; *P. versatilis* (Berk.) comb. nov. (*Trametes versatilis* Berk.) on Taxodium; *P. versicolor* (L.) Fr. on Liquidambar; *P. vinosus* Berk. on Liquidambar; *P. zonalis* Berk. on Carya, Celtis, Liquidambar, Populus, Quercus (La., Ark.). *Poria albocincta* Cooke & Massee; *P. ambigua* Bres. on Celtis and Liquidambar; *P. candidissima* (Schw.) Cooke; *P. eupora* Karst. on Quercus; *P. ferruginosa* (Schrad.) Fr. on Liquidambar; *P. flaccida* sp. nov. on Carya, Liquidambar, Taxodium; *P. inermis* Ell. & Ev. on Ilex; *P. Langloisiana* Murr. on Liquidambar; *P. Langloisii* Murr. on Fraxinus and Quercus (La., Ark.); *P. medulla-panis* (Pers.) Cooke; *P. nigrescens* Bres.; *P. punctata* Fr. on Carpinus and Fraxinus (La., Ark.); *P. undata* Pers. on Fraxinus; *P. versipora* Pers. on Ilex and Quercus (La., Ark.). *Solenia candida* Pers. on Taxodium. *Trametes cubensis* (Mont.) Sacc.; *T. malicola* Berk. & Curt.; *T. rigida* Berk. & Mont. on Fraxinus and Carya; *T. sepium* Berk.

The following species of Polyporaceae are deserving of further notice here:

Polyporus fimbriatus has not previously been reported from the North American mainland. Its relationships have been confused due to the fact that the hymenium develops very differently at different times, so that the species has been classed in both Thelephora and Hydnum, and previous southern collections have been referred as forms of the thin and variable *Polyporus tenuis* or its near relatives. It grows from buried rotted wood in large soft white tough imbricate clusters like *Stereum pargamenum*,

and in fact my photo of that species (fig. 4) represents it very well from the upper surface view. It occurred several times in late July and early August after abundant rains.

Polyporus fissilis Berk. Soft and watery, white throughout, cartilaginous within or forming mucilaginous or soapy masses in the crevices near the fruiting bodies, drying yellowish; context strongly zonate; pores medium-sized, the pore surface slightly lavender (figs. 5, 12, 13).

On living Liquidambar and on living Quercus, especially *Q. nigra* and *Q. Phellos*. Common in central and northern Louisiana and in adjacent Mississippi and Arkansas. Produces hollows in butts and lower trunks of living trees, preceded by a soft, ropy, general, cinnamon-colored or whitish decay of the heartwood, with persistent medullary rays. One of the most destructive heart-rotting fungi of the region, the decay either a butt rot or a trunk rot. Occasionally on logs down two or three years. Sporophores are frequently abortive, producing no tubes. The species is widely distributed in the eastern United States but northward it is very sporadic in appearance and has never been regarded as of any importance in Forest Pathology. Although observed many times in some stage of fruiting, no sporophores were seen that were not within reach from the ground, indicating that it is most frequently to be found as a butt-rot.

Polyporus ludovicianus (Pat.) Sacc. & Trott. This species has received little attention from mycologists. It was originally described from Louisiana. Lloyd considered it to be a form of *P. cuticularis*. Probably less than a dozen collections were known prior to 1931. We found it to be a rather common species and several collections were made. It grows in imbricate clusters after the manner of *P. sulphureus*, the clusters sometimes as much as 45 cm. broad. The entire sporophore is brown or rusty-ochraceous in color with thin applanate pilei, zoned and matted-tomentose on the upper surface. The spores are like those of *P. cuticularis*, brown in color, 5–6×

Fig. 5. Photo of cut in log of *Liquidambar styraciflua* showing hollow and rot produced by *Polyporus fissilis*, and at right and left masses of white fungous material of soap-like consistency taken from inside log at this point. Cut made at 19 ft. above stump. Greatly reduced.

Fig. 6. Showing advanced stage of rot in Liquidambar, as seen in tangential section view, caused by *Polyporus ludovicianus*. ×1.

Fig. 7. Heart rot in living Quercus, caused by *Polyporus sulphureus*. Greatly reduced.

Fig. 8. Imbricate sporophore mass of *Polyporus ludovicianus* growing on top of Quercus stump at Oak Grove, La. ×¼.

Fig. 9. Photo of heart rot in living Quercus, caused by *Polyporus lucidus*. ×1.

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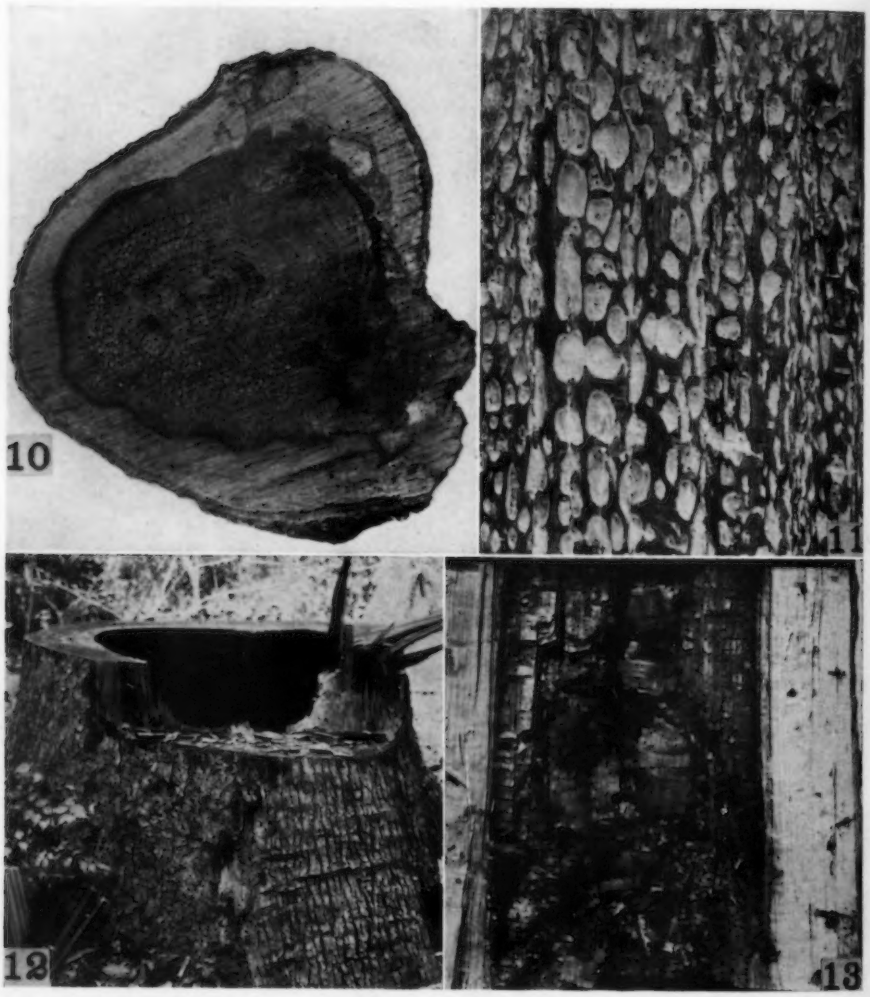

Fig. 10. Photo of cross section of log of Quercus with advanced stage of decay by *Polyporus hispidus*. $\times\frac{1}{4}$.

Fig. 11. Photo of large pocket rot in Quercus, probably produced by *Polyporus zonalis*. $\times 1$.

Fig. 12. Photo of stump of Liquidambar showing large hollow produced by *Polyporus fissilis*. This stump is of the same tree shown in Fig. 5. Greatly reduced.

Fig. 13. Advanced stage of rot of heartwood in Quercus, caused by *Polyporus fissilis*. The persistent medullary rays are characteristic of the rot on this host. $\times\frac{1}{3}$.

3.5–4 μ. Setae are not present and in this character it differs from the last-named species. It fruits only at the bases of living trees or quite as often on or about stumps of Liquidambar and Quercus. It produces a conspicuous speckled pocket-rot of the heartwood and seems to be one of the most destructive heart-rot organisms of the region. The pockets produced resemble those by *Stereum frustulosum* and *S. subpileatum*. The species proves to be rather widely distributed in the southern states, and collections are now known from South Carolina, Georgia, Alabama, Louisiana, and Texas (figs. 6, 8).

Polyporus persicinus Berk. & Curt. This species was originally described from South Carolina and has been collected but three or four times. Type fragments are said to be found at Kew and were studied by Murrill who reported that the description does not seem to apply to the type specimens and our present conception of the species is based on the type specimens rather than on the description. Coker twice collected the species at Chapel Hill, North Carolina, in this sense, and his specimens are at New York. I collected it once near Eudora, Ark. The species has considerable resemblance to the well developed centrally stipitate form of *P. distortus*. It grows on the ground though is probably attached to buried wood. The pilei are 10–25 cm. diameter, buffy-brown to pinkish brown when fresh but becoming sordid refescent-brown in age or on drying and the context of fresh specimens changes to a brownish-flesh-color where exposed, and is very friable and pale-brown on drying.

Polyporus radiatus var. **Cephalanthi** n. var. Sporophore practically resupinate, with only a tumid margin, yellowish-brown, tough; context brown; pore surface dark brown, the tubes 1–3 mm. long, their mouths averaging 4 to 5 per mm.; setae present, many with curved tips; spores nearly or quite hyaline, 4–4.5×3.5–4μ.

On dead standing *Cephalanthus occidentalis*. Common in northern and central Louisiana and at Eudora, Ark. Observed at many different stations. Never found with more than a suggestion of a pileus, which, together with the unusual and restricted habitat and the hooked setae almost make it worthy of specific recognition, especially since *P. radiatus* is not known to occur in its pileate form so far southward.

Polyphorus sulphureus var. *cincinnatus* Morgan. Forming imbricate or rosette-like clusters 10–50 cm. broad, the pilei salmon-colored above, white below, fleshy at first, finally brittle; otherwise it resembles the species except that it always occurs at the bases or on the roots of living trees of Quercus, apparently from the ground, but in reality producing a pseudosclerotium, often of considerable length leading to infested roots. This

pseudo-sclerotium exudes milky drops where broken. The present form is described in more detail by Rosen (Mycologia **19:** 191. 1927) August. Collected but once, at Oak Grove, La. Produces a carbonizing cubical rot of the heartwood (fig. 7). When heartwood heavily infested by the mycelium of this fungus is cut into, drops of a milky fluid collect on the cut surface of the wood.

Poria flaccida n. sp. Resupinate, annual, entirely white or drying cream-colored, soft and watery when fresh, drying rather soft; margin white, myceliod and cobwebby over the adjacent bark; subiculum very thin and delicate, cottony, white; pore surface even, the tubes up to 1 mm. long, their mouths angular, thin-walled, entire, averaging 3 to 4 per mm.; spores almost exactly globose, smooth, hyaline, 4–4.5×4μ; cystidia none; basidia 4–5μ diameter; hyphae flexuous, simple or sparingly branched, thin-walled and flaccid, with frequent cross walls but no clamps, diameter 2.4–3μ in trama, 3–4μ in subiculum.

On old logs of Carya, Liquidambar, and Taxodium. Louisiana. Type collected near Kilbourne, La., Aug. 14, 1931, on Carya log (U.S.D.A. For. Path. Herb. 50356; Overholts Herb. 14073); also collected near Ferriday, La. This species is a close relative of *P. ambigua* Bres. but differs in the globose spores and the somewhat smaller hyphae.

A genetic analysis of the inheritance of fragrance of gladiolus.

FORMAN T. MCLEAN

This study was undertaken for the purpose of developing and intensifying fragrance in the gladiolus. Two of the ten or more fragrant species of the genus *Gladiolus*—i.e. the highly variable *G. tristis* and equally variable *G. recurvus*, were intercrossed and records were kept of their progeny in the first and second generations and in a back-cross, to learn the mechanism of inheritance of fragrance in them. In all 2,200 individuals were studied, comprising 194 crosses. Fairly complete descriptions were made of these, and this mass of data was tabulated under twenty-five characters, two of which are of fragrance; a night fragrance derived from *G. tristis* and a violet-like daytime fragrance from *G. recurvus*. The clones of the two species used were apparently homozygous for the characters for fragrance, but for many of the other characters they were evidently heterozygous. This was to be expected, since the wild forms of both species vary greatly in color and markings, but have characteristic fragrance, and leaf and sheath characters.

Through the liberal cooperation of the officers and personnel of the Works Progress Administration, whose assistance it is a pleasure to acknowledge, this material was tabulated and compared in detail. The statistics were handled by Mr. Erwin Jarmel, who did excellent work on it. Only one phase is treated here.

The results clearly indicate that the two primary types of fragrance are inherited differently. The lily-like night fragrance of *G. tristis* is apparently recessive to the absence of it, and dependent on two factors for its transmission, one of which must be homozygous for its expression, but the other heterozygous. The violet-like recurvus fragrance is dominant and appears to require two factors, both of which may be heterozygous. Recurvus fragrance is also epistatic to tristis fragrance in certain combinations. Of the twenty-three other characteristics recorded, only four have evident relationships to fragrance; two to tristis fragrance, one to recurvus, and one to both. Considering the heterozygosity of these other factors, no linkage groups can be postulated here to further substantiate or tend to disprove the two-factor hypothesis for the inheritance of each type of fragrance. But the evidence for it seems sufficient in itself.

Two new types of fragrance, each more pronounced than the primary species types, were found in the hybrids. Further studies of these to learn their manner of inheritance, and studies of the transmission of fragrance to crosses of these species hybrids with the garden varieties of gladiolus are in progress. Both show promise.

REVIEW OF LITERATURE

There has been comparatively little breeding work to develop or intensify scent in flowers, and most of the workers have left no record of the inheritance of scent, except in very broad generalizations. Hampton[1] summarizes these observations. A preliminary report of the present work with gladioli was printed in 1933.[2] As already noted there, this was not the first attempt to produce fragrant gladioli. Dean Wm. Herbert reported the same cross in 1818 in a letter to the Royal Horticultural Society, London[3] and he subsequently named his hybrids *Gladiolus fragrans*. But that was long before the days of modern genetics, and there is no evidence that he carried the experiment beyond the first generation.

One reason for the lack of information on inheritance of fragrance is the inexactitude of the standards for odors and the mixed character of most of the natural ones, which are usually made up of several odors blended together. Hampton (loc. cit.) classifies odors of plants into ten groupings: (1) Indoloid or foetid, as in *Stapelia* and other carrion flowers; (2) Animoid or stale, as in hawthorn blossoms; (3) Heavy and sweet, as in jasmine; (4) Aromatic or sweet and spicy, as in clove carnation, night scented tobacco, etc.; (5) Violet or orris; (6) Rose; (7) Lemon, as in oranges and magnolias; (8) Fruit scented, as in *Philadelphus microphyllus;* (9) Animal and unpleasant, as in the lizard orchid; (10) Musk and honey, as in the musk plant and musk orchid.

Of these ten groupings, the fragrances dealt with here are:

I—*Gladiolus tristis* scent, a night scent belonging to class (4) Aromatic, possibly combined with some of class (7) Lemon.

II—The "Violet" scent of *Gladiolus recurvus* which is the strongest early in the morning and persists during the day, obviously belongs to class (5) Violet, possibly with other modifying elements in it.

Derived from these are:

III—"Lemon" scent, a daytime scent found in some of the hybrids, and:

IV—"Pungent," another daytime scent, occurring principally among the F_2 and later crosses.

Each of these four scents is clearly distinguishable, both by its time of occurrence, day or night, and by its dominant odor component, but it is quite probable that each is not a simple odor, rather a combination of

[1] Hampton, F. A. "Flower scent," pp. 104–106. London, 1925.

[2] McLean, Forman T. "The inheritance of fragrance in *Gladiolus* species crosses," Jour. N. Y. Bot. Garden **34:** 73–80. 1933.

[3] Herbert, Wm. "Instructions for the treatment of *Amaryllis longifolia* as a hardy aquatic, with some observations on the production of hybrid plants, etc." Trans. Hort. Soc. London, **3:** 187–196. 1820.

two or more. For each plant recorded, the quality of the fragrance is set down according to the above groupings, and its intensity, whether faint, medium or strong. Observed differences in intensity are not treated in the present analysis; the personal element enters too strongly into the perception of scent, as recently proven by the studies of Blakeslee[4] All of the observations of fragrance here reported were made by the author, with the corroboration of two co-workers, Miss Helene Lunt and Mrs. Harry A. Jennison, whose perceptions of scent were about the same as his. If the work had been done by a number of people, differing in the keenness of their perceptions, such consistent results would not have been possible; a person with keener sense of smell might have detected scent where the author did not, as actually happened in the case of a gladiolus scent not discussed here. On the other hand, many visitors proved to be insensitive to one or the other of the odors treated in this paper. So the results reported may be regarded as simply one man's consistent observations.

RESULTS

This study was begun at the Rhode Island Agricultural Experiment Station in 1925, and continued at the New York Botanical Garden from 1928 to 1937. The Boyce Thompson Institute for Plant Research, through the kindness of Dr. Crocker, worked out for me the pregermination cold treatment necessary for the germination of the seeds of these small gladiolus species and hybrids, the chemical treatments to break the dormancy of gladiolus corms, and the effect of supplemental light on blooming time.

The results here reported were based principally on hybrids derived from one clon each of *Gladiolus tristis* and of *Gladiolus recurvus*. A second clon of *G. recurvus* was used for the production of some first generation hybrids, and these are treated separately for comparison.

The *G. tristis* used is designated Tristis II, and was obtained from C. G. Van Tubergen & Co. as *G. tristis concolor*. The flowers are clear greenish cream, large for the species, and only two to four on each spike. The general characteristics of this clon, which was used as the seed parent of all of the F_1 hybrids here treated, are given in detail in the discussion after table 1.

The *G. recurvus* clon used principally in this study is called Recurvus Bronze, and was obtained from A. J. Kruijff, of South Africa, who called it the best and strongest growing form of the species. In greenhouse culture

[4] Blakeslee, Albert F. "Demonstration of differences between people in the sense of smell," Scientific Monthly **41:** 72–84. July, 1935.

here it is a weak grower, like all of *G. recurvus*, with rather flatter greyish leaves than the type, and light purplish bronze flowers instead of the typical violet or cream.

In series #55 of the first generation hybrids, a second clon of *G. recurvus* was used, called Recurvus Violet Purple. This was typical of the species.

In table 1, the distribution of the twenty-five recorded characteristics, including those for fragrance, are compared in the first generation hybrids, in series #55 (columns 2 and 3), in which Recurvus Violet Purple was the pollen parent; in series #60 (columns 4 and 5), in which Recurvus Bronze was used; in the second generation (columns 6 and 7), derived from series #60; and a back-cross in which F_1 #60 was recrossed with Tristis II. In the discussion of the results as given in the table, the characteristics of the species clons used as parents are also taken up.

The columns headed "N" give the number of individuals in each category. Observations are incomplete for certain characters of a few individuals, so that the total records on many characters do not add up to the total number of individuals studied, but the number of such omissions is believed to be not great enough to seriously affect the percentage distributions.

TABLE 1

Inheritance of twenty-five observed characters in first generation, second generation and back-cross of Gladiolus tristis and Gladiolus recurvus

No. of Records	First Generation F_1 #55		First Generation F_1 #60		Second Generation F_2 #60		Back-cross Tristis II × F_1 #60	
	191		192		362		284	
	N	%	N	%	N	%	N	%
Character								
0. No. of Flowers								
One	40	21.5	12	6.8	88	26.4	65	22.9
Two	89	47.9	75	42.6	168	50.5	156	54.9
Three or More	57	30.6	89	50.6	77	23.1	63	22.2
1. Height/Length								
Plus	10	5.3	45	27.3	64	17.8	97	33.9
Minus	180	94.7	120	72.7	296	82.2	189	66.1
2. Flower Size								
$\frac{1}{2}''$ to $1''$	5	2.8	19	10.9	50	14.6	0	0
$1\frac{1}{8}''$ to $1\frac{5}{8}''$	75	43.1	84	48.0	196	57.1	32	12.0
$1\frac{3}{4}''$ to $2\frac{1}{4}''$	89	51.3	72	41.1	91	26.5	184	68.9
$2\frac{3}{8}''$ to $2\frac{7}{8}''$	5	2.8	0	0	6	1.8	51	19.1
Statistical Average	1.76		1.62		1.54		2.14	
P. E. Average	.02		.05		.01		.01	

TABLE 1—*Continued*

No. of Records	First Generation F_1 #55		First Generation F_1 #60		Second Generation F_2 #60		Back-cross Tristis II× F_1 #60	
	191		192		362		284	
Character	N	%	N	%	N	%	N	%
3. Color of Flower								
Creamy	62	32.4	117	61.6	117	32.3	121	42.3
Creamy White	113	59.2	68	35.8	147	40.6	125	43.7
All Others	16	8.4	5	2.6	98	27.1	40	14.0
4. Shape of Flower								
Open	121	63.7	62	33.9	115	32.0	248	86.7
Intermediate	7	3.7	24	13.1	39	10.8	17	6.0
Bell	62	32.6	97	53.0	206	57.2	21	7.3
5. Tube Length								
$\frac{1}{2}''$ to $1''$	40	30.8	29	38.7	104	36.6	15	8.5
$1\frac{1}{8}''$ to $1\frac{1}{2}''$	81	62.3	45	60.0	168	59.2	76	42.9
$1\frac{5}{8}''$ to $2''$	9	6.9	1	1.3	12	4.2	83	46.9
$2\frac{1}{8}''$ to $2\frac{5}{8}''$	0	0	0	0	0	0	3	1.7
Statistical Average	1.29		1.22		1.23		1.60	
P. E. Average	.02		.04		.01		.01	
6. Tube Shape								
Curved	15	39.2	50	64.9	122	43.6	109	60.9
Straight	79	60.8	27	35.1	158	56.4	70	39.1
7. Segment Tip								
Pointed	169	88.5	130	88.7	317	87.8	283	99.3
Blunt	22	11.5	15	10.3	44	12.2	2	.7
8. Segment Width								
Narrow	26	13.7	46	34.8	101	28.2	165	58.3
Intermediate	9	4.7	22	16.7	76	21.2	43	15.2
Wide	155	81.6	64	48.5	181	50.6	75	26.5
9. Petal Texture								
Wavy	112	59.3	99	61.5	206	57.4	164	57.7
Plain	77	40.7	62	38.5	153	42.6	120	42.3
10. Flower Color Graining								
Plus	134	70.9	91	49.7	171	47.2	15	6.0
Minus	55	29.1	92	50.3	191	52.8	234	94.0
11. Flower Color Blotch								
Plus	174	91.6	119	62.0	258	71.3	209	74.1
Minus	16	8.4	73	38.0	104	28.7	73	25.9
12. Flower Lines to Tip								
Plus	150	78.9	143	78.1	234	64.8	146	51.2
Minus	40	21.1	40	21.9	127	35.2	139	48.8
13. Throat Lines								
Plus	122	64.6	66	50.8	225	62.3	251	88.1
Minus	67	35.4	64	49.2	136	37.7	34	11.9
14. Throat Dots								
Plus	171	90.5	76	58.5	205	56.8	91	32.0
Minus	18	9.5	54	41.5	156	43.2	193	68.0

TABLE 1—*Continued*

No. of Records	FIRST GENERATION F_1 ♯55		FIRST GENERATION F_1 ♯60		SECOND GENERATION F_2 ♯60		BACK-CROSS TRISTIS II× F_1 ♯60	
	191		192		362		284	
	N	%	N	%	N	%	N	%
CHARACTER								
15/16. TYPES OF FRAGRANCE								
Non-fragrant	4	2.0	7	3.7	135	37.3	111	39.1
Recurvus Scented	185	97.0	182	94.8	188	51.9	53	18.7
Lemon Scented					2	.5	2	.7
Pungent Scented					18	5.0		
Tristis Scented	2	1.0	1	.5	6	1.7	90	31.7
Recurvus and Tristis			2	1.0	8	2.2	17	6.0
Tristis and Lemon					3	.8	3	1.0
Tristis—Day and Night					2	.6	8	2.8
17. ANTHER COLOR								
Colored—Plus	183	96.3	139	80.3	215	59.7	168	59.2
Pale—Minus	7	3.7	34	19.7	145	40.3	116	40.8
18. PISTIL COLOR								
Colored—Plus	130	85.5	5	3.2	48	14.8	28	9.9
Pale—Minus	22	14.5	153	96.8	277	85.2	255	90.1
19. PISTIL LENGTH								
Plus Anthers	38	43.2	11	26.2	87	35.8	76	54.3
Equal Anthers	41	46.6	26	61.9	112	46.1	53	37.8
Minus Anthers	9	10.2	5	11.9	44	18.1	11	7.9
20. LEAF NUMBER								
One	36	61.0	129	73.3	265	73.4	186	65.5
Two	23	39.0	45	25.6	93	25.8	98	34.5
Three or more			2	1.1	3	.8		
21. LEAF SECTION								
Cross—Plus	30	15.8	18	9.8	52	14.4	235	82.5
Intermediate	147	77.4	152	83.6	253	70.1	50	17.5
Flat—Minus	13	6.8	12	6.6	56	15.5		
22. LEAF COLOR								
Greyish-Green	181	94.8	158	96.3	328	91.1	71	25.1
Yellowish-Green	10	5.2	6	3.7	32	8.9	212	74.9
23. LEAF SHEATH COLOR								
Brown	169	89.4	150	89.8	270	77.4	159	56.8
Intermediate	15	7.9	14	8.4	61	17.5	100	35.7
Green	5	2.7	3	1.8	18	5.1	21	7.5
24. LEAF SHEATH DOTS								
Plus	190	99.5	164	98.2	239	68.5	133	46.8
Minus	1	.5	3	1.8	110	31.5	149	53.2

Of the twenty-five characters treated in table 1, most of them appear to be either heterozygous in the parents of the plants studied, or so irregular in their distribution that they do not indicate any definite trend. The most promising characters are those for fragrance, which show con-

sistent and clear-cut results. These are analyzed more fully in table 2.

The parent of series #60, Recurvus Bronze, appeared to be heterozygous for character 4, shape of flower; character 8, segment width, narrow and intermediate being opposed to wide; character 10, flower color graining; character 13, throat lines; and character 14, throat dots. In each of these instances, the parent of series #55, the more typical Recurvus Violet Purple, seems to be more homozygous, judging by the F_1 hybrids studied.

For characters 17, 21, 22, 23 and 24, the results in all of the different groups appear much more consistent. Characters 23 and 24 show distributions such as would point to simple dominance of one factor for each.

Taking up the characters a little more fully:

0. The two parent forms of Recurvus and Tristis II, each have two to four flowers per spike, and the hybrids average two flowers each.
1. The ratio of height of flower stalk to length of longest leaf is consistently negative, and follows the tendency of *G. recurvus*, which is short stalked, while *G. tristis* is long.
2. Tristis II is large flowered, averaging $2\frac{1}{2}$ inches in diameter, while Recurvus averages $\frac{3}{4}$ to 1 inch. The hybrids are intermediate.
3. The flower color is predominantly creamy white, leaning toward the color of *G. tristis*.
4. Tristis II is distinctly a wide open flower, while Recurvus is more bell shaped. The hybrids are again intermediate.
5. A long perianth tube, 2 inches long, is a character of Tristis II, while Recurvus Bronze and Recurvus Violet Purple both average about $\frac{3}{4}$ inch. The hybrids are intermediate.
6. The curvature of the perianth tube is highly variable, and shows no clear inherited tendency, except that Tristis is curved.
7. The pointed segments of *G. tristis* are strongly epistatic over the blunt segments of Recurvus.
8. Wide segments, more than half as wide as long, are characteristic of Recurvus in contrast with the narrower segments of Tristis II. If narrow and intermediate are contrasted with wide, and Recurvus Bronze is assumed to be heterozygous for one of two dominant factors for wide, Tristis II and Recurvus Violet Purple being homozygous for wide and for narrow segments respectively, the distribution found closely approximates what would be expected, which is 100% wide in F_1 #55, 50% wide in F_1 and in F_2 #60, and 75% intermediate and narrow in the back-cross.

9. The perianth of Tristis II is plain, not wavy or ruffled, while that of Recurvus is inclined to be wavy, and this tendency slightly predominates in the hybrids.
10. Tristis II has a clear color, without markings. Recurvus is usually grained and stippled with darker color over the cream or creamy white ground color. In this case, both of the Recurvus parent forms appear to be heterozygous for the character for graining, Recurvus Bronze the more so.
11. Dark blotches on the three upper segments are characteristic but not invariable in *G. tristis*. Tristis II lacks blotches, and Recurvus in all its forms has narrow center lines or none. Despite this, blotches appear to preponderate in all groups.
12. Dark central lines to the tips of the segments of the flowers are characteristic of Recurvus Violet Purple, and most Recurvus, but do not occur in Tristis II. The tendency for these lines is evidently somewhat heterozygous in both forms of Recurvus. The back-cross shows a typical 1:1 ratio, possibly indicating this character to be a simple dominant.
13. The lower lip of Tristis II has greenish central lines in the throat, while Recurvus does not. No definite tendency can be detected in this case.
14. Dark dots on the lower lip at the throat characterize most forms of Recurvus; Tristis II lacks dots. Recurvus Bronze is evidently heterozygous for this character, which, from the distribution shown in table 1, and the linkages to characters for fragrance, discussed later, is assumed to depend on two supplementary dominant factors.

15 & 16. These characters refer to fragrance. Under 15 are recorded "day-scented" flowers. These include (1) violet scented flowers, with a fragrance like Recurvus by day, which are strongly dominant in the first generation, but do not appear in the F_2 and back-cross in the proportions expected for a simple dominant factor; (2) Lemon scented, appearing among the F_2 and back-cross, both alone and in combination with Tristis scent at night. This is evidently a derived scent, not found in either of the wild forms used, and is too scantily represented here to permit analysis of its inheritance. (3) Pungent scent, mildly resembling that of a carnation, is another derived scent, and found to the number of 18 (5%), only in the F_2, neither in F_1 nor back-cross. This would seem to argue for an affiliation with Recurvus scent. Under 16

are recorded "night-scented" flowers, which have the strong lily-like scent of *G. tristis* either alone or combined with other scents by day. This character is distinctly recessive in the F_1, and less represented in the F_2 and back-cross than would be expected of a simple recessive allelomorph to Recurvus scent. The proportions of these scents among the different groups, and the large number of non-fragrant hybrids in the F_2 and back-cross, though derived from scented parents and grandparents, exclude the possibility of these traits being inherited either as allelomorphs or as simple independent characters. In the next section an hypothesis is presented which successfully accounts for all of the findings. Discussion of this will be deferred until that is taken up.

17. Dark-colored anthers are characteristic of Recurvus, and while Tristis II had pale anthers, dark color in them is frequent in other forms of *G. tristis*. Anther color is dominant in the F_1, but only to the extent of 80% in the F_1 #60. If we may assume both Recurvus Bronze and Tristis II to be heterozygous for a dominant factor for anther color, this would quite reasonably account for the findings, except for the absence of it in Tristis II.
18. Recurvus Violet Purple had a violet colored pistil, and this character was evidently dominant in the F_1. Recurvus Bronze and Tristis II both had pale pistils.
19. Tristis II has the pistil longer than the anthers, and Recurvus has it shorter. The hybrids are intermediate.
20. The number of fully developed leaves per plant is normally two in Tristis II, but one in Recurvus; and the one-leaf predominates in the hybrids.
21. The leaf cross-section is cruciate in Tristis II, but flat in Recurvus. The hybrids are quite definitely intermediate, except the back-cross, which leans strongly toward the Tristis form.
22. Tristis II has a normal bright yellowish-green leaf color while Recurvus has greyish-green, which is dominant in the F_1, just as strongly represented in the F_2, but only 25% are greyish-green in the back-cross. The genetic explanation of this type of distribution is not clear.
23. The color of the leaf sheath is brown in both Tristis II and both clons of Recurvus, so would be expected to dominate the hybrids.
24. The leaf sheath of *G. recurvus* is characteristically dotted with pale greyish dots on a basic green or brown color. This dotting

is apparently a simple dominant over the uniform sheath color of Tristis II, the two F_1 series being dotted 98 and 99½% respectively; 68½% dotted in the F_2, approaching a 3:1 ratio; and 47% dotted in the back-cross, nearly a 1:1 ratio, as expected for a one-factor dominant. None of the other characters show such a simple relationship. But the characters for fragrance show interesting trends, which are next considered in detail.

INHERITANCE OF FRAGRANCE

If it is assumed that two supplementary factors, designated for convenience R and S, either or both of which may be heterozygous, are necessary to develop recurvus fragrance; that two other supplementary factors, located on different chromosomes and designated T and U, are both necessary, one heterozygous and the other homozygous, to develop tristis fragrance; and that recurvus fragrance is epistatic to tristis fragrance in certain combinations; and further that lemon and pungent are combinations containing tristis fragrance factors; then this hypothesis will account within 2 per cent of error, in all except the first generation, for all of the results given in table 2, which compares the actual inheritance distribution with the computed values based on these assumptions.

Tristis II would then have the genetic formula rrssTTUU, and Recurvus the formula RRSSttuu, with respect to fragrance alone. The small letters, r,s,t and u represent the non-fragrant allelomorphic factors to the fragrance factors, R,S,T and U, respectively. In the hybrids, all having at least one R and one S will also have recurvus fragrance; and those having one T with two U's will have tristis fragrance. But it is further assumed that recurvus fragrance is epistatic to tristis fragrance to such a degree that in the presence of both R and S, homozygous T as well as homozygous U is necessary to bring out both recurvus and tristis fragrances in one individual. Thus RrSsTTUU, or RRSsTTUU, or RrSSTTUU, or RRSSTTUU would carry both recurvus fragrance by day and tristis fragrance at night. But RrSsTtUU would show only recurvus fragrance, despite the fact that individuals with TtUU without R and S together would have tristis fragrance, as would all those with TTUU, regardless of R and S. The computed values in Table II are based on this hypothesis.

The possibility that the ten percentage values, for recurvus scent in two groups of first generation hybrids, of non-fragrant, recurvus scented, recurvus and tristis scented, and of tristis scent with other combinations, would all except two fall within two per cent of the expected percentages, and that even these divergent values would not deviate more than 4 per cent from those expected, without the hypothesis being true, seems very

TABLE 2

Comparison of inheritance of recurvus and tristis fragrance with expected values based on two factors for each

	FIRST GENERATION		FIRST GENERATION		SECOND GENERATION		BACK-CROSS	
	F_1 #55 Tristis II× Recurvus, V. P.		F_1 #60 Tristis II× Recurvus, bronze		F_2 #60 F_1 #60× F_1 #60		Tristis II× F_1 #60	
No. of Plants recorded	191		192		362		284	
Column A—Actual % Column C—Computed %	A	C	A	C	A	C	A	C
1. Non-fragrant	2	0	3.7	0	37.3	35½	39.1	37½
2. Recurvus scented	97	100	94.8	100	51.9	52¾	18.7	18¾
3. Recurvus and Tristis	0	0	1.0	0	2.2	3½	6.0	6¼
4. Tristis scented	1	0	.5	0	1.7	*	31.7	*
5. Lemon scented	0	0	0	0	.5	*	.7	*
6. Pungent scented	0	0	0	0	5.0	*	0	*
7. Lmon and Tristis	0	0	0	0	.8	*	1.0	*
8. Tristis, day and night	0	0	0	0	.6	*	2.8	*
* Total, Tristis, Lemon and Pungent combined					*8.6	*8¼	*36.2	*37½

* Note: These totals are of items 4 to 8 inclusive; Tristis, Lemon, Pungent and combinations of these.

remote. With from two hundred to four hundred individuals recorded in each group, a deviation of 2 per cent from the calculated values is about the normal variability. There seems, therefore, to be no need to assume a more complex or a very different hypothesis from the one proposed to account for the inheritance of the two primary types of fragrance. This explanation does not account for the lemon and pungent scents, except to place them with the tristis group.

RELATION OF OTHER CHARACTERS TO FRAGRANCE

To see if there were any indications of linkage of any of the twenty-three other characters to fragrance, all of the data of second generation and later hybrids, (excluding the first back-cross to tristis, Group #152) comprising in all 852 individuals were tabulated with respect to fragrance, and presence or absence of each of the twenty-three other characters, and the material was summarized, showing percentage of the plants possessing a given type of fragrance which also possess a given other character. Then the coefficient of contigency[5] for each of the most strongly probable re-

[5] See, Davenport, C. B. and Ekas, M. P. Statistical Methods, 4th Revised Edition, John Wiley & Sons, 1936.

lations was worked out. The detailed results are not presented here, as they did not prove significant for the present study, except that nine characters numbers 4,6,8,10,12,14,21,22 and 24, (see discussion of table 1 for detailed description of these) showed a strong coefficient of contingency, exceeding .100 in value, for a relationship of the other character to tristis or recurvus fragrance. It is noteworthy that in each of these instances, in every case the porportion of individuals with a given fragrance which also have the character is high, sixty to ninety per cent (see table 3), but the converse of this is not true—that is, of the total number possessing the apparently linked character, the proportion also possessing the fragrance is always less than fifty per cent. To test the significance of these apparent relationships, and to find whether they may represent true linkages between the other characters and fragrance, the 852 indivuals were subdivided into six inheritance groups, designated studies 1 to 6 respectively, as follows:

Study #1 N—362 Second Generation Tristis II × Recurvus Bronze
Study #2 N—173 Second Generation of #152 (Back-cross to Tristis)
Study #3 N—74 Second × Third Generation of #152
Study #4 N—54 Second Back-cross to Tristis (Tristis × #152)
Study #5 N—62 Cross between First and Second generation
Study #6 N—127 Cross between First and Second Generation of Back-cross #152

A portion of this material and a small amount of scattered supplemental data was then lumped into two groups, one consisting of individuals with equal contibutions of *G. tristis* and *G. recurvus* to their pedigrees, and a second group in which all of the individuals have a preponderance of *G. tristis* in their pedigree, as follows:

Group I. Revised study #1 comprises 362 F_2 #60.
Individuals and study #5 comprises 62 individuals of a cross F_1 #55× F_2 #60, making a total of 424 individuals.
Group II. Derivatives of the Tristis back-cross #152 crossed with each other and with other groups, consists of 374 individuals.

Group I is thus equally *G. tristis* and *G. recurvus* in inheritance, while Group II is $\frac{5}{8}$ or more *G. tristis* and shows strong dominance of *G. tristis* characters.

Any apparent linkage of one character with another may be influenced by dominance of that character, so that two dominant characters may appear to be linked with each other when they really are not. In such instances, if the linkage does not persist in back-crosses in which either or both characters are relatively less frequent, then the apparent linkage is believed not to be significant.

The results of these groupings are given in table 3. In column 1 are

given the characters by number, as described earlier, column 2 gives a statement of the premise for a linkage, columns 3 and 4 give data for the total of 852 cases; in column 3 the norm, that is the percentage of the total group possessing the given character and in column 4 the percentage of the scented individuals also possessing the other character. Thus on line 1, column 3, 51.6 means 51.6 per cent of the individuals in the total group have open shaped flowers, and in column 4 the 79.0 means 79.0 per cent of the individuals with tristis scented flowers in this group also have open flowers. Columns 5 and 6 give similar data for Group 1, and columns 7 and 8 for Group II.

TABLE 3

Linkage of other characters to tristis and recurvus fragrance

CHARACTER NO.	FINDINGS	TOTAL GROUP N-852 C. NORM	%	GROUP I STUDY #5 REVISED STUDY #1 N-424 C. NORM	%	GROUP II STUDY #2-3-6 N-374 C. NORM	%
4	Tristis Scented Flowers Are Open Shaped	51.6	79.0	30.8	28.6	71.4	82.5
	Recurvus Scented Flowers Are Bell Shaped	32.9	50.8	56.4	59.1	10.3	15.2
	Coefficient of Contingency	.374		.017		.175	
6	Tristis Scented Flowers Are Curved Tubed	55.3	66.7	45.1	57.1	61.7	70.5
	Recurvus Scented Flowers Are Straight Tubed	44.7	51.1	54.9	55.2	38.3	38.6
	Coefficient of Contingency	.161		.051		.095	
8	Tristis Scented Flowers Are Narrow Petaled	43.8	70.9	27.9	42.8	56.7	69.9
	Recurvus Scented Flowers Are Wide Petaled	34.7	51.6	51.3	54.7	20.0	39.1
	Coefficient of Contingency	.409		.096		.395	
10	Tristis Scented Flowers Lack Graining	68.3	96.5	52.4	85.7	82.3	96.8
	Recurvus Scented Flowers Are Grained	31.7	49.0	47.6	50.5	17.7	43.5
	Coefficient of Contingency	.378		.131		.444	
	Tristis Fragrance	N 86	10.1	N 67	1.7	N 63	16.9
	Recurvatus Fragrance	N 252	29.6	N204	48.1	N.47	12.6

TABLE 3—*Continued*

CHARACTER NO.	FINDINGS	TOTAL GROUP N-852 C. NORM	%	GROUP I STUDY #5 REVISED STUDY #1 N-424 C. NORM	%	GROUP II STUDY #2-3-6 N-374 C. NORM	%
12	Tristis Scented Flowers Lack Lines to Tip	50.6	61.6	35.9	14.3	63.5	60.3
	Recurvus Scented Flowers Have Lines to Tip	49.4	60.6	64.1	65.2	36.5	41.3
	Coefficient of Contingency	.191		.075		.017	
14	Tristis Scented Flowers Lack Throat Dots	55.2	80.2	45.2	85.7	60.2	74.6
	Recurvus Scented Flowers Have Throat Dots	44.8	63.3	54.8	62.7	39.8	67.4
	Coefficient of Contingency	.354		.177		.386	
21	Tristis Scented Are Cross Leaf	46.5	89.5	15.8	42.9	74.7	92.1
	Recurvus Scented Are Interm. or Flat Leaf	53.5	81.1	84.2	84.7	25.3	47.7
	Coefficient of Contingency	.538		.172		.346	
22	Tristis Scented Are Green Leaved	28.1	54.7	11.1	28.6	44.8	55.6
	Recurvus Scented Are Gray Leaved	71.9	90.7	88.9	92.6	55.2	81.4
	Coefficient of Contingency	.418		.141		.346	
24	Tristis Scented Lack Sheath Dots	46.2	63.1	30.0	42.9	58.4	59.0
	Recurvus Scented Have Sheath Dots	53.9	69.5	70.0	75.3	41.6	45.5
	Coefficient of Contingency	.279		.068		.046	
	Tristis Fragrance	N 86	10.1	N 7	1.7	N63	16.9
	Recurvus Fragrance	N252	29.6	N204	48.1	N47	12.6

In table 3 is shown the linkage of other characters to tristis and recurvus fragrance expressed by means of a coefficient of contigency. Character 21—Leaf Section—shows the strongest linkage to fragrance (C. = .538) and table 4 shows in detail how this coefficient of contingency was computed.

TABLE 4

Note: Selections made from a total group of 852 hybrids.

	TRISTIS FRAGRANCE	RECURVUS FRAGRANCE	
Cross Leaf Section	77	47	124
Intermediate and Flat Leaf Section	9	202	211
	86	249	

$$\frac{1}{86}\left(\frac{5929}{124}+\frac{81}{211}\right)=.5599$$

$$\frac{1}{249}\left(\frac{2209}{124}+\frac{40804}{211}\right)=\underline{.8480}$$

$$P.=1.4079$$

$$\sqrt{\frac{.4079}{1.4079}}=\sqrt{.2897}=C..538$$

In order to determine the coefficient of contingency we had to obtain first a measure of probability called P from the square contingency, which may be interpreted by means of a coefficient of contingency. The most valuable form is that derived by Pearson, which he has called C_2 or which we may call C. In its interpretation C is identical with the "product moment coefficient of correlation." It should be particularly noted that if we employ only two classes as the established means of our coefficient of contingency the highest possible coefficient may be only .707; table 4 therefore clearly shows that the relationship; tristis scented flowers are cross-leafed and Recurvus, scented flowers are intermediate or flat-leafed, is a valid one.

A comparison of linkage of these characters to tristis and to recurvus fragrance, expressed as percentage of the total tristis or recurvus fragrant hybrids possessing the character shows as follows:

Character 4. Flower Shape, shows in Group I a relationship of bell shape of flower to recurvus scented—59.1 per cent; both of these characters are strongly represented in this group, but only 15.2 per cent of the recurvus scented are bell shaped in Group II, which is predominantly open rather than bell shaped. The apparent linkage in Group I is reversed in Group II. Tristis scented flowers in Group II show 82.5 per cent open shaped flowers, only 28.6 per cent however in Group I. The apparent relationship of 79 per cent for the total group is not borne out in both sections of it. Accordingly we can only assume there is no consistent linkage of flower shape to either tristis or recurvus fragrance.

Character 6, flower tube curvature, is by similar reasoning to the above, weakly related, curved tube to tristis scented, in Group II 70.5 per cent. Group I, with very few tristis scented plants, shows 57.1 per cent of tristis scent with curved tube. But the converse, straight tube to recurvus scent shows no relationship.

Character 8, narrow petaled, are represented amongst tristis scented 69.9 per cent in Group II, and 42.8 per cent in Group I, which has few of narrow petaled and still fewer tristis scented. Again the converse relationship to recurvus scent is not found.

Character 10, darker graining on the petals, fails to show relationship to recurvus fragrance, being nearly half and half, with and without graining in Group I, Group II and the Total Group. But the absence of graining is strongly represented among the tristis scented plants, 96.8 per cent in Group II, 85.7 per cent in Group I and 96.5 per cent in the Total Group.

Characters 12, 21, and 24 all show reversals in apparent relationships in the two groups, with regard to tristis and recurvus fragrance.

Character 14, throat dots on the lower lips of the flower, also show a weak relationship, 62.7 per cent and 67.4 per cent in the two groups respectively, while the converse shows even a closer relationship and linkage, 85.7 per cent and 74.6 per cent respectively.

Character 22, leaf color, shows close relationship of recurvus scent to gray leaf 92.6 per cent and 81.4 per cent respectively but none of tristis to green leaf.

Thus of the nine characters showing a 60 per cent or greater apparent linkage to tristis or recurvus fragrance in the Total Group, only four of them, nos. 6, 10, 14 and 22 show this consistently in Groups I and II. Let us consider the minimum group relationship as most nearly the true one—and this is reasonable, since in breeding with this material, selection of parents was entirely for fragrance, the other characters not being given any consideration, so that they may be regarded as random selections with regard to all except fragrance.

Then tristis scent may be regarded as linked to curved tube (character 6) 57.1%, and to lack of graining (character 10) 85.7%. In each of these cases no converse relationship to recurvus fragrance is found. This further supports the hypothesis already stated that the factors for tristis and for recurvus scent are not allelomorphs. But in the case of character 14, tristis scented lack throat dots 74.6%, and recurvus scented have throat dots 62.7%, thus showing an apparent relationship to each fragrance. If throat dots are dependent on two dominant factors, so that the absence of throat dots is linked to one factor for tristis and the presence

of them is linked to one for recurvus fragrance, it would then fulfill the requirements in this instance. By reference to table 1 the proportion of throat dots found in the first and second generations and back-cross would fit in well with this assumption also, if we assume that the parent of F_1 #55, i.e. Recurvus Violet Purple, is homozygous for each of two factors for throat dots, but that the parent of F_1 #60, Recurvus Bronze, is homozygous for one factor for throat dots, but heterozygous for the other. Grey leaved is apparently linked to recurvus scented, recurvus scented being grey-leaved (character 22) 81.4%, but not tristis scented to green leaved.

The relationship of tristis scented to other characters in Group I is insecure in each case, being based on only seven tristis scented individuals, but the other relationships, based on 47, 63 and 204 individuals respectively, may be regarded as reasonably sure.

CONCLUSION

1. From a study of hybrids of *G. tristis* with *G. recurvus* consisting of F_1, F_2 and a back-cross of $F_1 \times$tristis, it was found that the violet-like fragrance of *G. recurvus* was dominant, and the aromatic night scent of *G. tristis* was recessive.

2. In the F_2 and the back-cross two new types of fragrance were observed and designated lemon scented and pungent scented.

3. From a study of the proportions of each type of fragrance and combinations of them in the different groups of hybrids, and from the occurrence of large proportions of scentless F_2 and back-cross hybrids it is assumed that each primary type of fragrance is a resultant of the influence of two independent genetic factors, such that two dominant factors are necessary for the expression of recurvus scent, and a dominant and recessive factor for the expression of tristis scent.

4. A preliminary survey of the relationships of the other recorded characters to those for fragrance indicate that the factors for curved flower tube, and for absence of graining of dark color on the flowers are linked each to one factor for tristis scent, that the factors for spotted throat of the flower are linked to both tristis scent and recurvus scent, and that grey leaf color is strongly linked to recurvus scent.

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INDEX TO AMERICAN BOTANICAL LITERATURE
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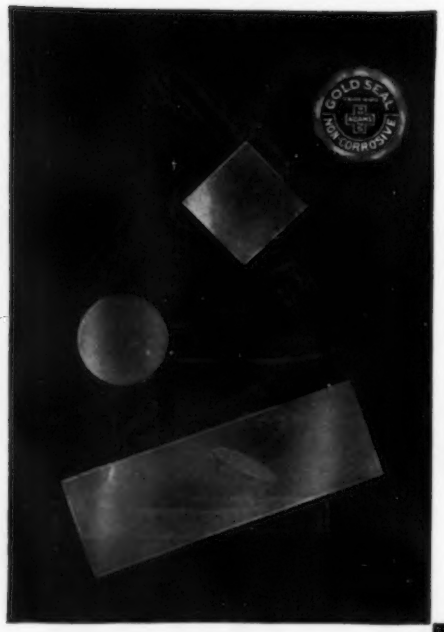

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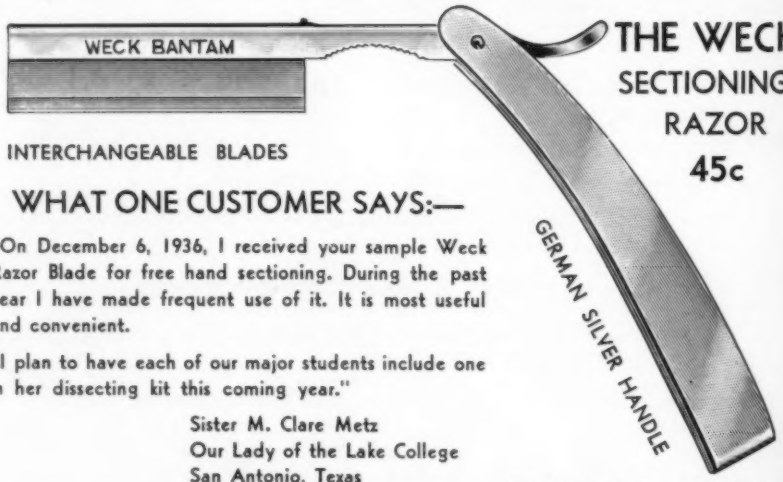

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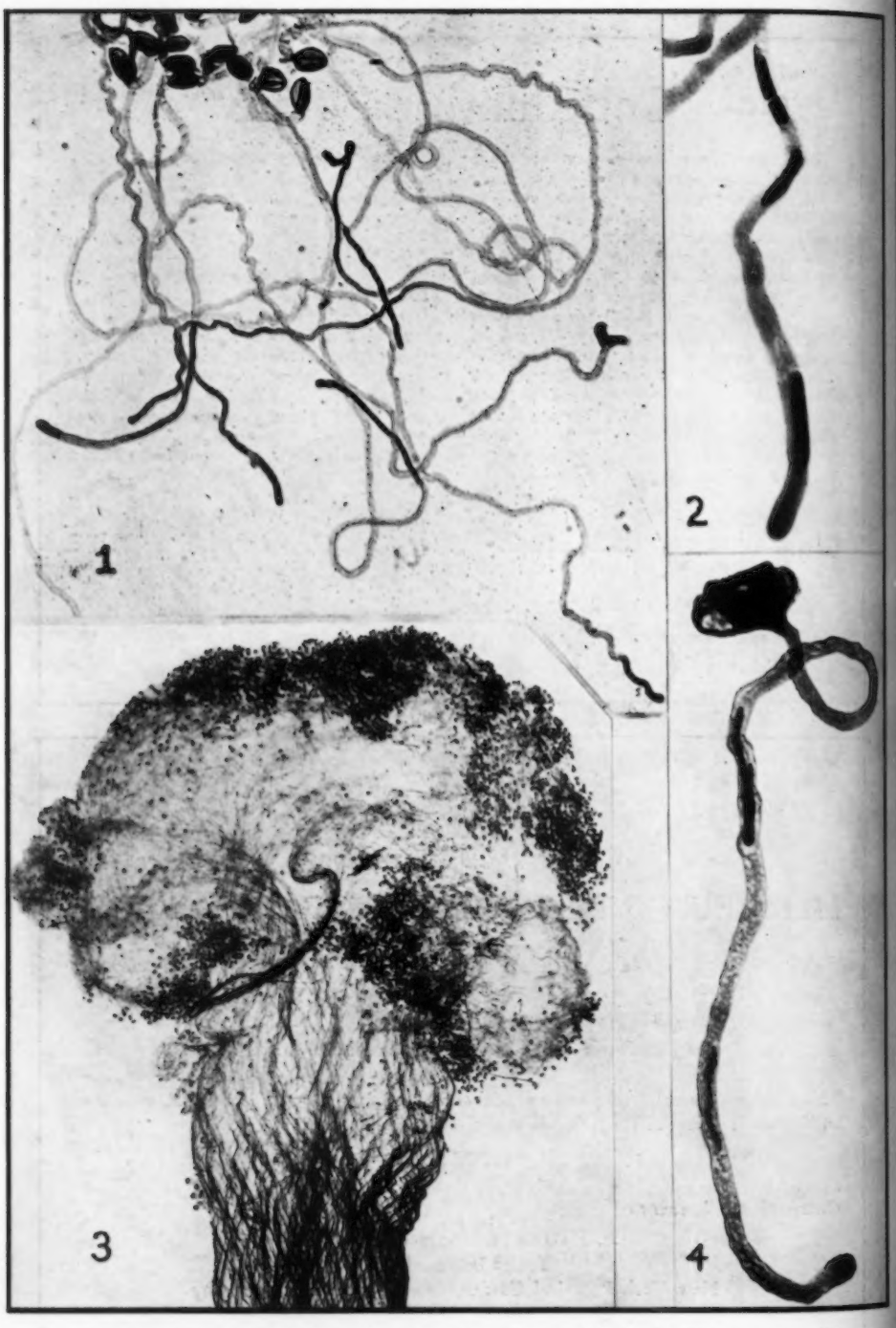

Figure 1: General view of germinating pollen of **Polygonatum.**
Figure 2: Enlarged view of above, showing tube nucleus and male gametes.
Figure 3: Style dissection of **Lilium,** showing pollen tubes.
Figure 4: **Tradescantia,** tube nucleus and generative nucleus.